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ANIMAL BREEDING

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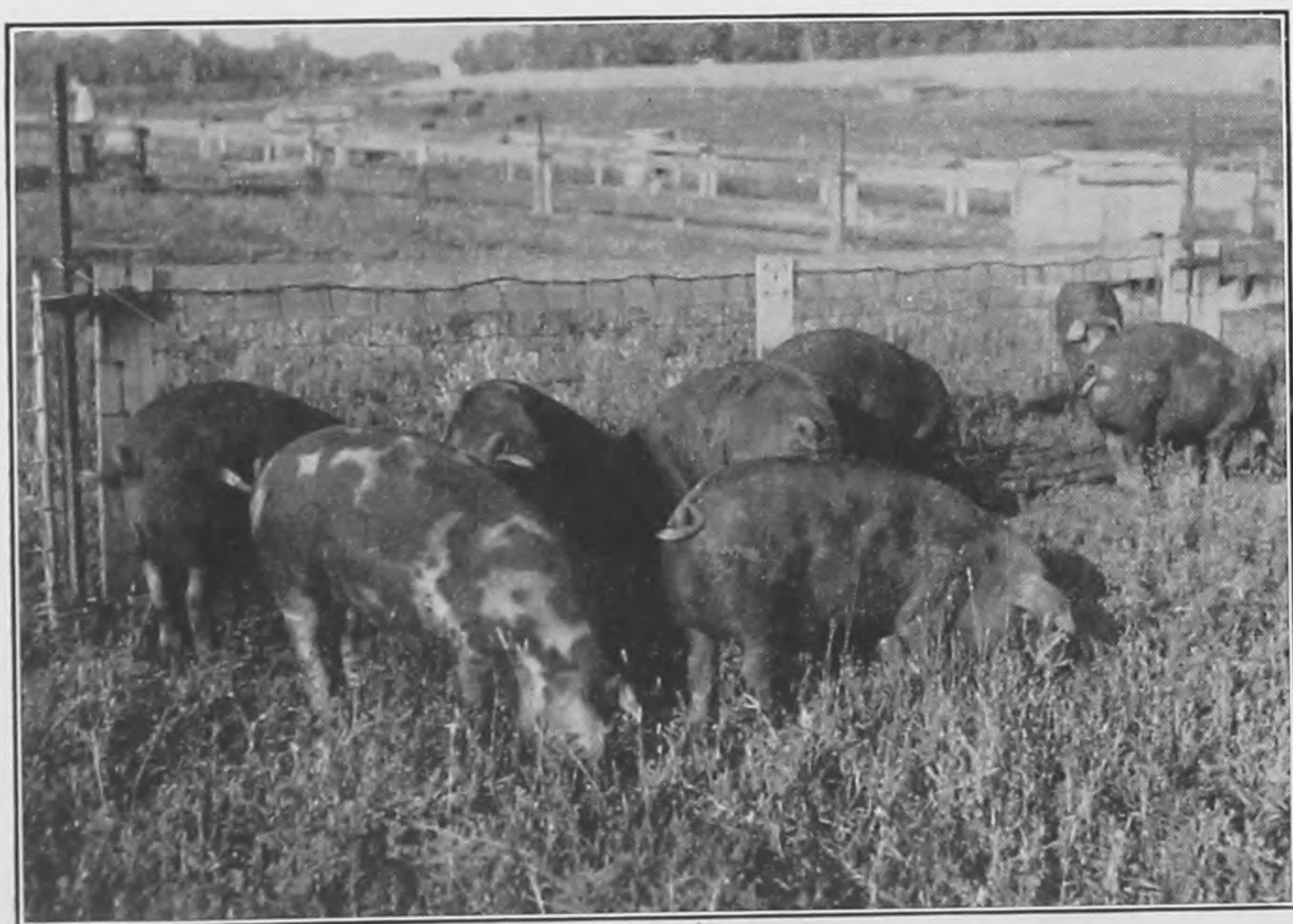
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The final measure of the value of a system of breeding is what it produces. Two groups of market swine produced from crossing inbred lines: (a) Minnesota C \times Minnesota No. 1; (b) Minnesota No. 2 \times Minnesota No. 1.

ANIMAL BREEDING

LAURENCE M. WINTERS

*Late Professor of Animal Husbandry
University of Minnesota*

with

Chapters on
Selection and the Effectiveness
of Selection

by WILLIAM REMPEL

*Assistant Professor of Animal Husbandry
University of Minnesota*

and

Chapters on
Fertility and Artificial Insemination

by JOHN N. CUMMINGS

*Associate Professor of Animal Husbandry
University of Minnesota*

FIFTH EDITION



ASIA PUBLISHING HOUSE

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LONDON • NEW YORK

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BY

LAURENCE M. WINTERS

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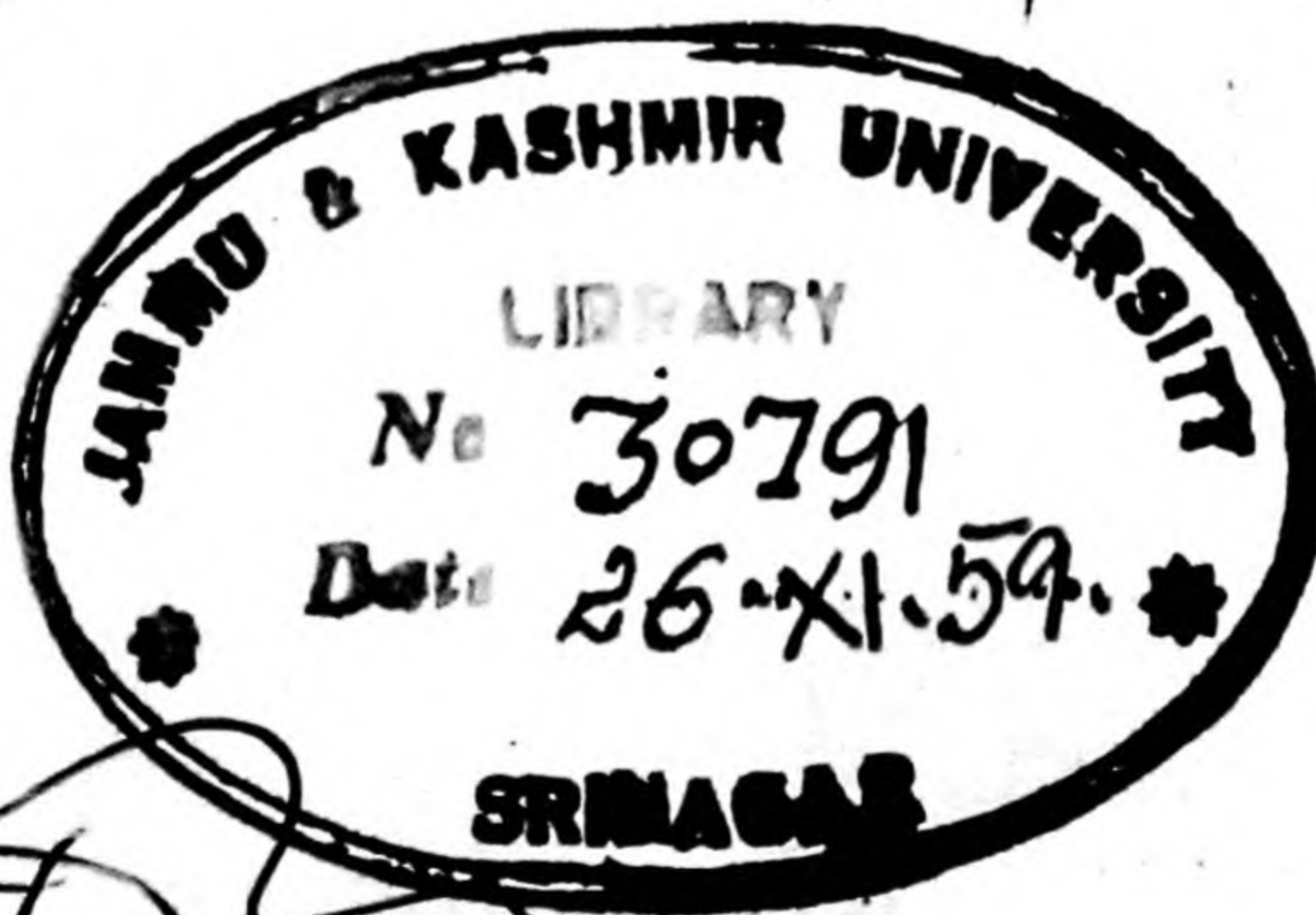
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FIFTH EDITION

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Preface

Our understanding of the basic principles involved in and their applications to breeding animals has been increasing at a rapid rate during this century. Each revised edition of this book is an attempt to keep pace with this increased information. In a field as young as animal breeding it is natural that there should be differences of opinion as to the best application of basic principles to applied breeding. It is logical that I should put my own views in the foreground since these convictions are the results of my own experiences, observations, studies, and meditations. This I have done; to do otherwise would be a negative approach.

This edition, like the previous ones, was prepared primarily for a beginning course in the teaching of animal breeding at the college level. It is intended that the student should have had a beginning course in genetics and some basic study in biology. I am well aware that not only students but all of us forget and fail to apply basic information to practical problems; hence as in previous editions this one contains a review and suggested applications of genetics and the physiology of reproduction to the breeding of animals.

I have also attempted to write to and for the progressive practical breeder. Many men in the field are anxious to widen their understanding of animal breeding. This and the above paragraph naturally include the agricultural high school teacher and the agricultural county agent.

The more introductory portions of the book have been left much as they were, but additions and substitutions have been made. The discussion of lethals was revised. The chapters on Selection, Effectiveness of Selection, Inbreeding, Crossbreeding, Purebred Breeding, Fertility, Artificial Insemination, and Building Superior Germ Plasm have been completely rewritten. All were rewritten to include recent contributions to the field. The chapter on Building Superior Germ Plasm was expanded materially.



In preparing this edition I have been aided materially by my

two colleagues, Drs. J. N. Cummings and William Rempel, each of whom supplied two chapters and in addition made many valuable suggestions and assisted in editing the manuscript. I appreciate the generosity of other authors and publishers in permitting the use of the illustrations.

LAURENCE M. WINTERS

St. Paul, Minnesota
January, 1954

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The Economic Importance of Animal Improvement

Farm animals fill an important place in man's scheme of life. Their function is to convert raw materials into more refined products which are of more direct use to man. Rough feeds are of little, if any, direct use to man, but when animals have converted them into meat, milk, and wool they become practically indispensable to modern man's existence. Meat and milk possess nutritive properties not available in plants; man has found many special uses for wool and fur.

It, therefore, becomes the function of a sound animal husbandry to produce these varied animal products as economically as possible. Animal breeding is only one of the steps in the process of animal production but, as it is the first step, it is fundamental to a sound animal husbandry. As time advances it becomes increasingly important for the conversion of raw materials into animal products to be made more and more economical. One reason for this is that, as the world's population increases and the soil becomes more worn, increased efficiency becomes of increasing importance. Another reason is that competition from synthetic products and foreign agriculture are constantly on the increase.

Substitutes for Animal Products. During recent years many synthetic substitutes for animal products have been developed. Some furnish quite satisfactory replacements for products that were once thought obtainable only from animals. Several of the vitamins that were once obtainable only in animal products are now being made in laboratories. Clothing is being made from glass and wood.

Synthetic products have introduced many interesting types of substitution: vegetable oils and animal body fats have been substituted for butterfat, casein for wool, soybean protein for casein,

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and yeast for lean meat. Less expensive furs, including lamb pelts, are being made to imitate expensive furs.

Fortunately for the animal producer, all these substitutes have proved, up to date, only *substitutes*; public demand has continued to prefer the original even at substantially greater costs, in many instances, because of the inferiority of the substitute article, and in other instances, because of flavor preference. On the whole, however, synthetic products give indications of providing continued competition rather than more outlets for animal products. As technology improves we may expect more synthetic products of improved quality at still lower costs.

Foreign Competition. The livestock producer like every other producer is always confronted with the competition of producers in other countries. This has become increasingly true with improvement in transportation. Modern transportation has brought nearly all corners of the world into competition with each other. The nation on an importing basis can bolster domestic prices through tariffs. However, the general history of tariffs on food products shows that once a nation is on a permanent importing basis a high tariff becomes unpopular with the majority of the population, and the tariff is removed or lowered. The history of the famous "Corn Laws" of Britain illustrate this point very adequately. That should sound a warning to American farmers, especially the livestock farmers, that in the long run their best means of retaining a prominent place in the sun is through an improved agricultural technology.

The Livestock Industry a Large One. The livestock industry of the United States is large. As both monetary values and livestock numbers fluctuate, it is impossible to be specific regarding the monetary values or the numbers of farm animals. The total livestock numbers for the United States run about 70,000,000 cattle, 84,000,000 hogs, 65,000,000 sheep and lambs, 4,000,000 mules, and 10,000,000 horses. This constitutes a huge basic industry in itself, and dependent on it are the meat packing, the dairy manufacturing, and the woolen industries, each of which in turn is a big industry.

For the entire United States over 50 per cent of the farmers' cash income is from the sale of live animals and animal products. In many of the best farming sections, livestock and livestock

products are responsible for 80 to 90 per cent of the farmers' cash income.

Animal breeding is the beginning or the foundation of this huge industry. No structure can be stronger than its foundation, hence it behooves agriculturists, livestock farmers especially, to give special attention to their program of animal breeding.

Animal Supply per Capita Not Large. A high standard of living is dependent on an adequate per capita supply of animal products. In spite of the huge livestock numbers in the United States the per capita allotment is not large, and since 1890 it has been on the decline. To raise the standard of living there will be far from enough animal products to satisfy domestic demands.

The United States ranks far ahead of the world average in this regard. If it becomes possible to raise the standard of living in the world as a whole, there will be an unprecedented demand for and shortage of animal products.

Merit of Average Livestock Too Low. This country possesses many fine herds of livestock, the equal of any in the world. On the other hand, many farmers still raise inferior stock. The result is that the average merit of the stock produced in this country is far too low. For the country as a whole the average butterfat production per cow milked is estimated to be only about 190 pounds. It is estimated that the average hen in this country lays only 90 eggs per year: a hen must lay a minimum of 120 eggs per year in order to be a profitable hen. The average hen is, therefore, only about three-fourths as productive as she should be to make a profit for her owner and in normal times is a liability to her owner.

Only about 84 lambs are raised per 100 ewes, and the average sow raises only about 6 pigs, whereas in a high-producing flock 150 lambs raised per 100 ewes is not unusual, and a good sow will raise from 8 to 10 pigs. The average wool clip per ewe for the nation is about 8 pounds, yet it is possible to get an average clip of 12 pounds or more.

The few recorded tests of the efficiency of feed utilization show clearly that feed requirements per unit of gain may be pared 25 to 50 per cent through the use of improved breeding

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coupled with improved management. Farm surveys have shown that hogs that make 100 pounds of pork from 450 pounds of feed are perhaps somewhat better than the average, yet it has been demonstrated that with crosses of improved inbred lines it is possible to produce 100 pounds of pork on 300 pounds of feed. (The foregoing has reference to gains made between weaning and market maturity.)

However, the fact that the efficiency of our farm animals can be improved materially is encouraging for the future of livestock production and proves that it is not necessary to allow either synthetic products or foreign competition to upset our livestock economy, provided we take advantage of improved technics. It is also encouraging for the development of increased outlets for animal products. Whereas synthetic products have been making inroads on animal products, new uses have been found for animal products. This is especially true of milk and the glandular organs. Price always has an important bearing on the utilization of goods, hence, if comparative costs are reduced, we may expect a greater demand for animal products.

On the whole it is clear that much remains to be done in regard to raising the level of livestock production in this country. During periods of inflation even the least efficient frequently make a profit, but in periods of deflation, or even during the few periods that can be called normal, only the superior producers usually have a profit.

Superior Livestock More Profitable. The term superior livestock may convey somewhat different meanings to different individuals. To the author, superior means a ewe that clips 12 or more pounds of wool and raises a pair of fast-growing market topping lambs annually; a sow that raises 10 pigs averaging 200 pounds in 150 days; or a dairy cow that produces 450 pounds of butterfat in a year on twice-a-day milking.

Nodland and Pond (1944 and 1945) have shown in farm surveys that there is a close relationship between the merit of livestock and cash returns. Table I shows the relationships between lambing percentage and lamb quality with returns.

In swine Nodland and Pond have demonstrated that the numbers of pigs weaned per litter and the pounds of feed required per 100 pounds of pork produced are closely identified with the returns over feed costs (Table II).

TABLE I. RELATIONSHIPS BETWEEN PER CENT LAMB CROP AND AVERAGE VALUE OF LAMB TO RETURNS OVER FEED COSTS

(From Nodland and Pond, *Minn. Bul. 382*)

Average Per Cent Lamb Crop	Number of Farms	Return over Feed	Average Index Value of Lamb	Number of Farms	Return over Feed
44	71	\$1.35	54	24	\$1.74
80	86	2.26	82	90	2.13
100	131	2.71	99	174	2.66
119	99	3.13	117	92	3.39
143	55	3.78	153	122	3.57

TABLE II. RELATIONSHIPS BETWEEN NUMBER OF PIGS WEANED PER LITTER AND THE FEED CONSUMED PER 100 POUNDS OF PORK PRODUCED AND RETURNS OVER FEED COSTS

(From Nodland and Pond, *Minn. Bul. 379*)

Average Pigs Weaned per Litter	Number of Farms	Return over Feed	Pounds Feed per Hundred- weight of Hogs	Num- ber of Farms	Return over Feed per Hundred- weight of Hogs
4.1	232	\$0.80	352	285	\$2.98
5.5	309	1.49	448	510	2.09
6.4	400	1.74	543	343	1.13
7.8	430	1.76	637	166	0.36
			864	115	-2.03

In dairying Nodland and Pond also show that the farmers with superior herds are the ones that reap the greater profit (Table III).

TABLE III. THE RELATIONSHIP OF BUTTERFAT PER COW TO RETURNS OVER FEED

(From Nodland and Pond, *Minn. Bul. 378*)

Average Butterfat per Cow	Number of Farms	Return over Feed
155	139	\$20.00
202	439	33.54
249	533	44.32
293	282	54.79
350	69	65.10

The above tables show very clearly, as has been previously demonstrated by the Ontario Department of Agriculture (1920)

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and Wilner (1925) in North Dakota, that good livestock is more profitable. In appraising these data it should be borne in mind, however, that the quality of livestock bred was probably not the sole factor responsible for the superior performance of the stock. The farmers with the better producing livestock are invariably the better caretakers. Nevertheless, the better caretaker usually has the better bred stock because he realizes its greater value.

General Procedure in Breeding Superior Animals. The farmer's problem resolves itself into how he is to proceed in breeding superior livestock. How to proceed is a big question and involves several considerations. In the past most improvement has been made through focusing attention on body form. Poultry and dairy cattle are two exceptions that might be cited, but even in these two classes of livestock much, if not most, attention in improvement has been placed on form or type. Only very recently poultry men have recognized two distinct types or subgroups within poultry breeds, namely, standard bred and production bred. Improvement has been accomplished through concentration on type, and much of the livestock of the nation could still be improved by giving more attention to form.

The livestock breeder of the future, the breeder who is going to elevate livestock breeding to new heights, will need to broaden his horizon, he will need to focus attention on other points in addition to body form and little details of type. As a first step he will do well to understand the fundamentals involved. The fundamentals in this case involve the basic principles of the physiology of reproduction and genetics and their applications to animal breeding and, in addition, an understanding of sound animal husbandry with an appreciation of its many problems.

Animal Breeding Defined. Genetics is the branch of biological science that seeks to account for the similarities and differences exhibited by related individuals. The physiology of reproduction is that branch of biology which deals with the processes by which new individuals come into being. *Animal breeding* is the application of genetics and the physiology of reproduction to animal improvement. In practice it calls for use of both the science and the art of breeding for further improvement.

Tools of the Animal Breeder. The animal breeder has only three basic tools: selection, crossbreeding, and inbreeding. The

task of modern animal breeding is to acquire mastery of these three tools. Since the establishment of the breeds attention has been focused chiefly on selection and on only a small portion of selection, namely, show type. The modern approach to animal improvement is much broader, and selection is based on records of performance, perfection of body form being only one of the items taken into account.

The purpose of using records of performance is to focus attention more directly to economy of production. In swine, sheep, and beef cattle it has been demonstrated that certain animals and strains will gain weight on 25 to 50 per cent less feed than others. The livestock breeder of the future cannot afford to ignore such differences; in fact, it is likely that in the not far distant future he will not be able to exist as a livestock producer if he ignores them.

In record-of-performance breeding, the breeder maintains records of the important items bearing on efficiency of production. In dairy cattle these items are milk production, butterfat percentage, feed consumption, and regularity of reproduction. In poultry they include egg production, egg size, fertility, hatchability, general vigor, rate of gain, and the marketable qualities of the young bird. In swine they include size of litter, livability, rate of gain, feed requirements, and quality as measured by market standards. In sheep the record includes regularity of reproduction, number of lambs born, number of lambs raised, quantity and quality of wool produced, the lambs' rates of gain, and quality, from the market standpoint, of the lambs produced. In beef cattle regularity of reproduction, rate of gain, feed costs, and merit of the animals produced for block purposes are the points to be considered.

Except with dairy cows not many breeders are in a position to maintain a detailed record of feed consumption per animal or per litter. The constructive breeder of the future will need to keep the other records indicated above. Progress has been made by selecting on the basis of form, but it is quite clear that in producing our best animals we have advanced as far as possible by past methods. With the aid of records, however, the breeder will be able to select breeding stock on the basis of performance and thereby do a better job of breeding more useful animals.

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Oddly enough, more progress has been made in getting the producers of commercial stock than purebred breeders to maintain records of performance. This perhaps is not odd since only about 3 per cent of the livestock is purebred; yet this situation should be reversed and it should not be necessary for the commercial producer to maintain detailed records. A national objective should be the development of strains of seed stock sufficiently bred for production so that the commercial producer could buy sires of this or that strain with the same degree of assurance that he buys a bushel of hybrid seed corn or a bushel of an improved variety of oats.

Crossbreeding and inbreeding were both used in the founding of the breeds, but later they came into disfavor. The livestock breeder of the future must understand the fundamentals involved and the technics whereby these tools can again be used more generally.

Heredity and Environment. Heredity refers to the transmission of characteristics (morphological, physiological, and psychological) from parent to offspring. The laws of heredity seek to account for the resemblances between related individuals, and also to recognize and explain the lack of similarity between related individuals. Not all the similarities between related individuals are attributable to their common relationship, for the common association of related animals accounts for many similarities. Common association accounts especially for similarities of mental traits. Animals that are wild teach their offspring and associates to be wild. Similar feed and care, especially if they have certain deficiencies, tend to bring about certain similarities within a group of animals.

The individual's attainment in life is, therefore, determined not by heredity alone but by environment as well. Figure 1 illustrates a five-day-old Hackney foal in action. The foal is already displaying remarkable action which is the direct result of its inheritance as environment has not yet had an opportunity to exercise an influence.

Figure 2 is a picture of a Hackney prize winner. With advancing age heredity became complemented by environment. The heredity had to be broad enough to allow the degree of development shown, and the environment had to be such as would allow the superior heredity to develop in full.

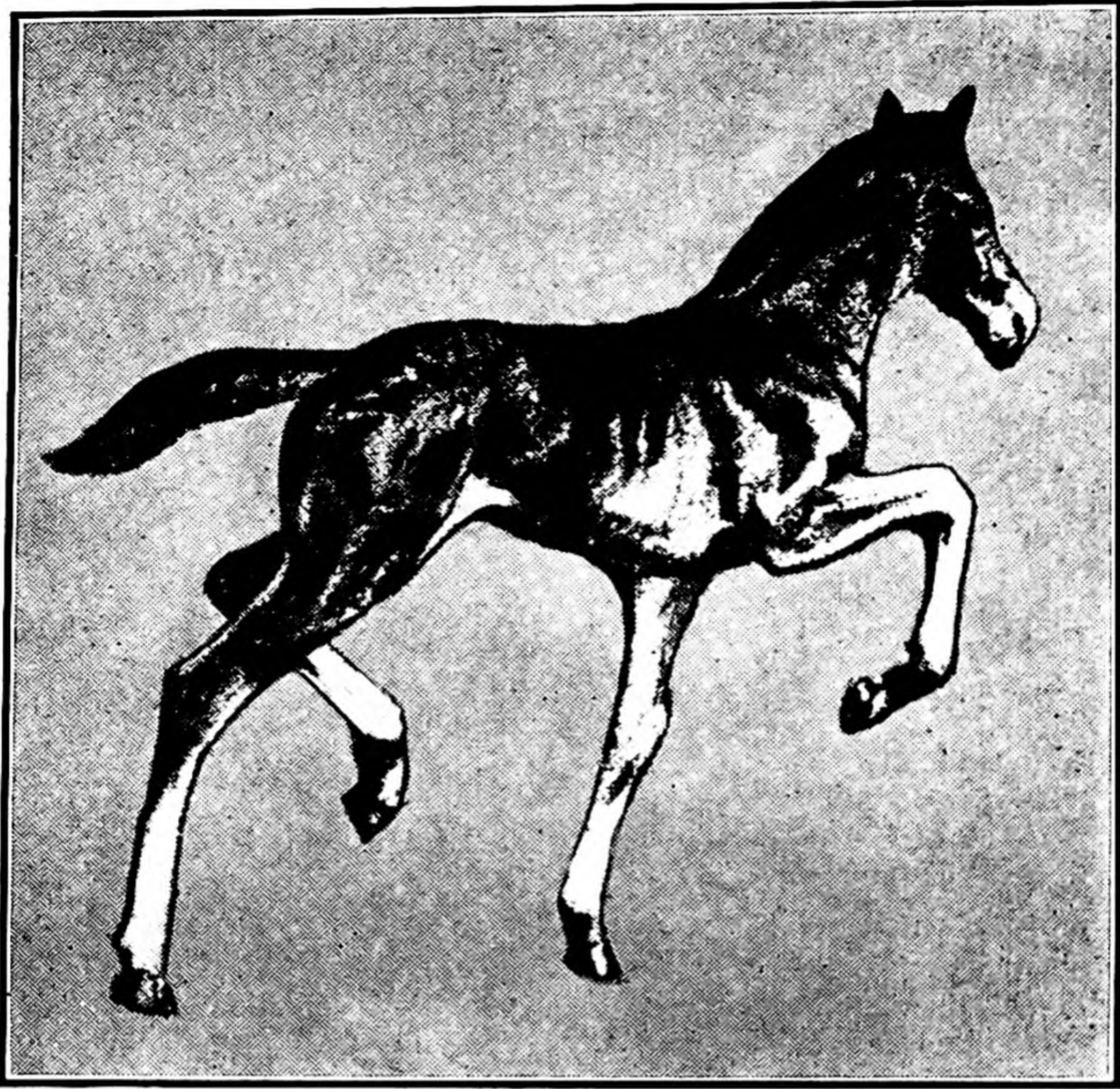


FIG. 1. A five-day-old Hackney foal showing remarkable action.

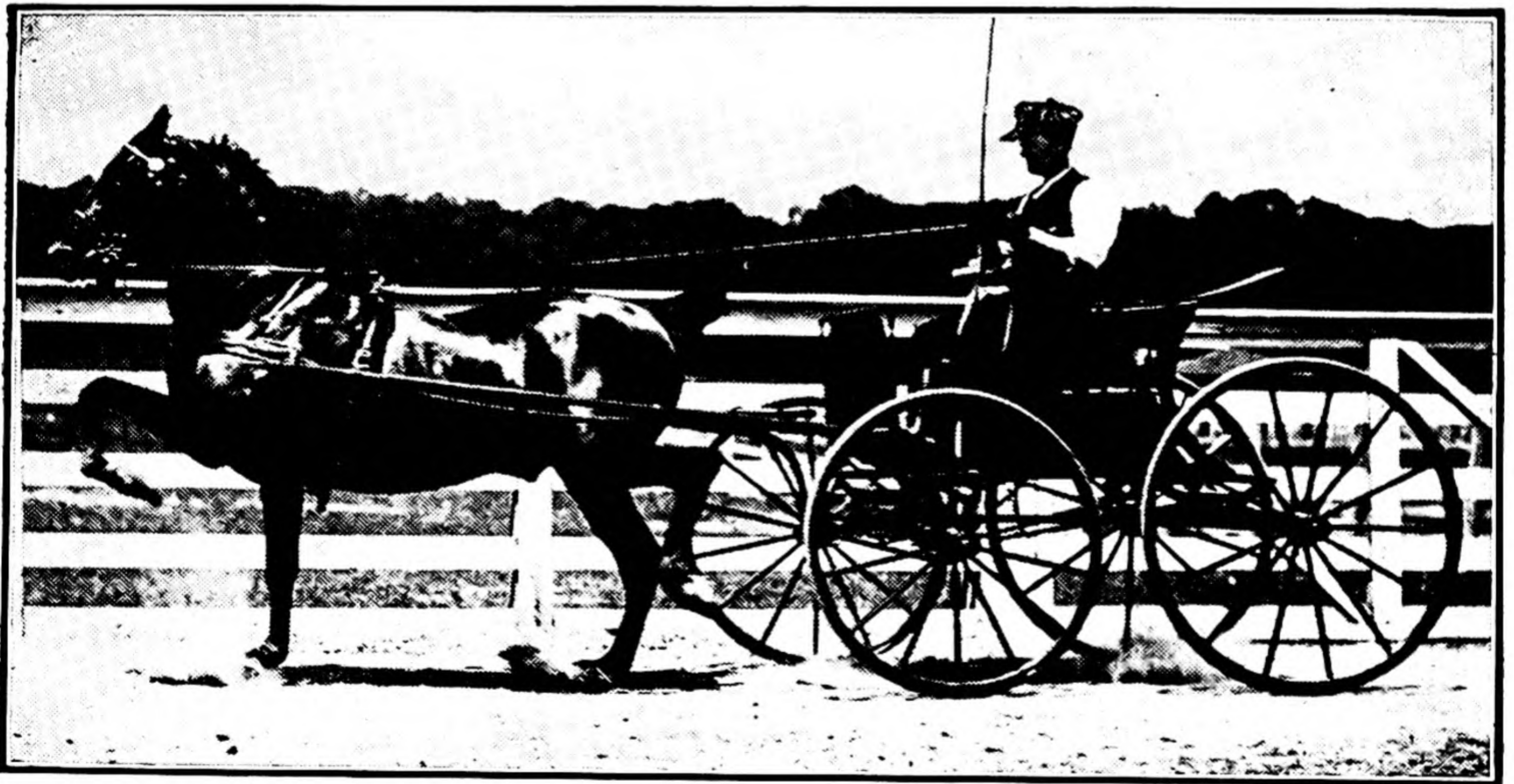


FIG. 2. A Hackney champion; the result of a satisfactory heredity and environment.

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A satisfactory picture of the interworkings of heredity and environment may be obtained if we visualize heredity as circumscribing the individual's future attainments, mental and physical as well as morphological. The relationship of heredity and environment is illustrated in Fig. 3; the circle represents the individual's hereditary possibilities and limitations at the time of fertilization; and the small dot represents the individual's attain-

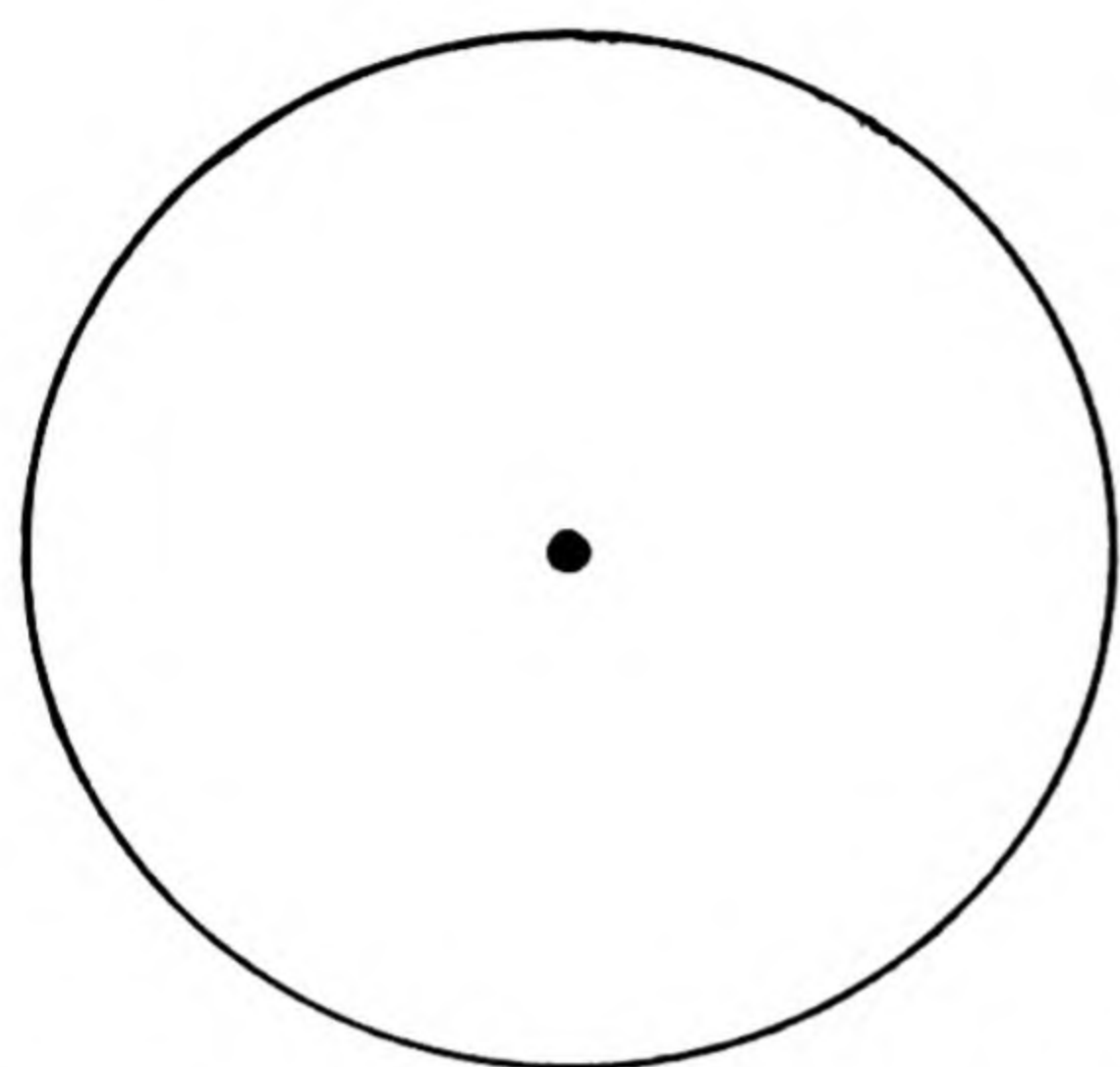


FIG. 3. Illustrating the interrelation of heredity and environment. The outer circle represents the new individual's possible attainments; the black dot, the individual's present attainment. (See text.)

ments at that time. A satisfactory environment is necessary for the individual to fill the circle, but in spite of its environment it cannot go beyond the bonds of its heredity.

Heredity, therefore, provides the foundation, and it may be likened to the foundation of a building. Environment is required to complete the structure, just as builders and materials are necessary to complete a building. As the type of foundation limits the type and size of building that can be built, so the heredity of a lamb limits the type and merits of the lamb that can be developed. The laying of a foundation for a building does not guarantee that the building

will be completed; nor does the possession of a desirable heredity guarantee that the individual will develop into an outstanding individual.

Necessity of Good Environment. Environment includes the sum total of all the external factors affecting the individual. It includes both quantity and quality of feed, housing, managerial practices, and the like. Regardless of the degree of superiority of the lines of breeding, the results will be disappointing unless the environment is also satisfactory. Too often well-bred animals are reared in faulty environments.

Overfeeding and pampering may prove as detrimental to the animal's well-being as underfeeding and lack of care. It is a wise livestock man who knows how far to go in this respect without either over- or underdoing his work. Here, then, is one of the places where the art of animal husbandry comes into play, be-

cause no one, no matter how skilled, can lay down hard and fast rules that will hold for all conditions. In fact, the type of feed and care required for best results will vary for different regions. In areas where land is high priced and feed is plentiful it is usually most profitable to full feed and force the animals almost to maximum capacity. The range country is in striking contrast; here it is usually most profitable to make maximum use of the cheap feed available, and this procedure will often curtail production. These two contrasted environmental conditions call for contrasted managerial practices. Each environment may call also for somewhat different inherent traits in the animals to meet the local conditions. Under more intensive farming conditions animals that are quiet and respond readily to heavy feeding will usually prove more profitable. Under range conditions hardihood may well prove the most valuable characteristic an animal can possess.

For best results in breeding, the environment should allow the animals' heredities to become expressed. This is necessary in order that selection may become most effective. Thus it is the breeders' business to develop strains of animals especially well suited to the conditions under which it is expected that the animals will be reared by the best commercial livestock producers of the area. The commercial livestock producer will in turn profit by purchasing sires that have been bred for production for his particular environmental conditions.

Relative Importance of Heredity and Environment. A frequently raised question is which is the more important, heredity or environment? The true answer will vary for the different traits within a given population and for a given trait in different populations. Studies of heritability have, for the most part, shown relatively low heritabilities in contrast to the influences of environment. These studies are reviewed later in the book, but in the appraisal of these and similar studies it should always be borne in mind that heredity is fundamental and that the individual cannot develop beyond its heredity. Environment is necessary in order to complete the structure; therefore, the breeder's job is to supply the best of both.

Control of Heredity. The livestock breeder's aim is to gain a maximum control over heredity. The breeder's ambition in mating animals is to exercise such a control over the matings that

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only the more desirable characters of each parent are transmitted to the offspring. A control as simple as this would indeed prove a panacea to the livestock breeder. But the problem of improvement is far from being so simple. The difficulty is that the new individual starts life from the union of two germ cells that are only about $1/125,000$ and $1/125$ of an inch in diameter. The actual determiners of an animal's inheritance are in the 40 to 60 chromosomes found within these tiny germ cells, and these determiners, known as genes, may run into the thousands in numbers. But the germ cells are produced by the animals used in mating; hence it is through an understanding of the fundamentals involved that the breeder may hope to gain control over the heredity of his animals. The fundamentals involve the three tools: selection, crossbreeding, and inbreeding.

CHAPTER II

Historical Background

The story of the development of our present farm animals is an interesting tale, but one of which, in a textbook of this kind, only a résumé is in order.

As judged by radium calculations, fossil remains carry the history of the horse back some fifty million years, according to Matthew (1926). In prehistoric times, the horse was widely distributed, remains having been found not only in Europe, Asia, and Africa but in North and South America as well. In fact, many consider America the original home of the prehistoric horse. By some chance he was lost to America long before its discovery by Columbus. Some consider that the North American horse perished or was pushed south during the glacial period and later perished owing to parasites and disease. Others attribute his disappearance to the carnivorous animals of the period. The ancestors of our present-day horse (termed "the dawn horse") ranged in size from that of a cat to that of a fox terrier. They had four toes on the fore foot, three toes and very small vestigial remains of the first and fifth digits on the hind foot, and teeth which were very short crowned and had but little enamel. By the process of evolution, presumably through ten stages of development (Table IV), there has been a gradual increase in size, a reduction in the number of toes, an increase in length of the teeth, and a thickening of the crown covering them. That the horse has gone through these stages of development has been well illustrated by the work of students in natural history.

The evolution of our other farm animals has not been worked out so completely; but, in every kind of animal, it is assumed that there has been a decrease in the number of toes and a deepening of the teeth and the covering over them. The explanation for this is that, as the world became drier and animals

TABLE IV. STAGES OF EVOLUTION OF THE HORSE

(After Matthew, *Quarterly Review of Biology*)

Period in Geological History	Formations	Stage of Development
Pleistocene	Glacial and Interglacial	10 Equus
Pliocene	Blanco	9 Plesippus
Lower Pliocene or Upper Miocene	Nebraska (Ogalalla)	8 Plihippus
Middle Miocene	Deep River	7 Merychippus
Lower Miocene	Harrison-Rosebud	6 Parahippus
Upper Oligocene	White River { Protoceras beds Oreodon beds Titanotherium }	5 Miohippus
Middle and Lower Oli- gocene		4 Meshippus
Upper Eocene	Uinta Washakie	3 Epihippus
Middle Eocene	Bridger Wind River	2 Orohippus
Lower Eocene	Wasatch	1 Eohippus

moved out of the swamps, the multiple-toed condition became a hindrance rather than an aid.

In swamp areas the spreading foot is an advantage because it gives footing; but on drier areas it is an encumbrance because it reduces speed. On dry land, the *survival of the fittest*, more than likely in many cases, went to *the swiftest of foot*. As for the teeth, dry-land being more fibrous than swamp vegetation, strong grinding surfaces developed.

Significance of Evolution. Evolution is a continuous process and is going on today but, for the most part, it is so slow and the changes are so small that we recognize only few. Evolution demonstrates that biological life is plastic and dynamic. Through the years different kinds of animals have evolved. Still further, although less drastic, changes have occurred during domestication and early constructive animal breeding. Natural selection or *survival of the fittest* has played a leading, perhaps the major, part in bringing about these changes. Natural selection could, however, do no more than weed out the less fit. Mutations and gene recombinations had to be at work so that new types, better suited to a changed environment, were evolved. Mutations may have been induced by environmental changes (this does not imply the inheritance of acquired characters). Recombinations have been stimulated by crossbreeding and inbreeding, both of which very likely occurred sporadically in nature.

The would-be constructive breeder may draw encouragement from all this, for his task is to speed up and control the very processes that have been occurring naturally. His first task is, therefore, to learn all he can of the laws governing these changes. If he is to be a constructive breeder, his task is to bring about new combinations of genes better suited to his purposes than existing combinations; his task is more or less to duplicate what nature has been doing but to do it with much greater speed and precision.

The Domestication of Animals. The domestication of animals began at a more remote period than the recorded history of man, for man's own evolution from savagery to domesticity is very directly associated with his domestication of, and association with, animals.

Shaler (1895) considers the dog the first animal tamed by man. According to him the dog was tamed not for material gain, but for the sake of companionship; it is very likely that for a long time the dog was used only for companionship and as a reserve food supply, for the dogs of savages are much like their masters—creatures of scant intelligence, and hence of little use to their masters. Gradually, however, as man's own intelligence increased, he made use of the dog, and consequently, by continued selection through the ages, a more useful type of dog was evolved. By still further selection and possibly with crossing, inbreeding, and further selection, the different types and breeds were developed.

Shaler considers that the horse was the next animal to be domesticated. Others consider the horse the last of our farm animals to have been tamed. However, there is good evidence that in the Paleolithic period the horse was widely distributed over Europe and Asia. There is also evidence, from the bones found in the caves of France and Belgium, that during this period the horse was one of man's chief supplies of food.

It has been assumed that man first followed animals in their migrations, as the American Indian followed the bison; and that man finally conceived the idea that by herding and caring for them during times of feed scarcity he would be more nearly assured of a food supply. As the ox and buffalo (Asiatic) became tamer, man perceived that he might use them as beasts of burden, and they were undoubtedly so employed long before the horse.

The camel and the elephant were also made use of at a very early date. Swine, sheep, and birds early attracted man's attention as sources not only of food but also of clothing.

It is generally considered that during the Neolithic period domestication proceeded fairly rapidly. Ridgeway (1905), however, considers it doubtful that man tamed the horse until after this period. There has likewise been some difference of opinion regarding how the horse was first used. Ridgeway presents good evidence that the horse did not serve as a mount until long after he was hitched to chariots. As a mount, he became greatly prized for war purposes, and gave his possessors a decided advantage over their unmounted adversaries.

At a very early date cattle, sheep, and goats were valued for milk production. It is very likely that these animals were completely domesticated before any others, for an animal needs to be tamer for dairy purposes than for hitching or riding. One of the bas-reliefs found in the tomb of Prince Mehenwetre of Egypt illustrates a cow being milked with all her legs tied securely. From this it has been inferred, by some, that the cow was not completely tamed even at that time; but this is no proof, for even at present cows often have their legs tied for milking, and the bas-relief may have been an illustration of milking a wild cow rather than the method of milking typical in that day.

Origin of Our Present Farm Animals. The only original wild horses, not the descendants of those which have run wild from domesticated studs, known to have existed in recent years are those which inhabit the steppes of Central Asia, known as Prejvalsky's horses, so called from the name of their discoverer. Many writers have considered this horse the logical ancestor of all our modern horses. Ridgeway (1905), however, traces the ancestry of our present horses to three distinct sources: the Prejvalsky horse of Central Asia, the Celtic pony of northern Europe, and the Libyan horse of northern Africa. This explanation is accepted by both Gay (1913) and Matthew (1926). Ridgeway believes that the Celtic pony is the ancestor of our present pony breeds; that our draft breeds are the result of more or less mixing of the Libyan and Prejvalsky stock; and that our light horses rest almost directly upon the Oriental group, which in turn rests directly upon the Libyan foundation. Ridgeway presents a vast array of both historic facts and citations,

tracing color and quality to prove his theory. According to him the Libyan horse was possessed of considerable quality and refinement long before the dawn of history. This is not at all incompatible with facts regarding present-day wild animals for the deer and the elk, among others, possess much quality and refinement. It merely means, at least for certain types of animals, that there is an advantage in the possession of quality and refinement and that through the years natural selection directed their evolution that way.

Many breeders of draft horses have inclined to believe that their breeds are indigenous stock of their ancestral homes. According to Ridgeway's interpretation, draft horses are the result of crossing the two ancestral stocks, Prejvalsky and Libyan. According to this interpretation our draft horses owe their refinement to their Libyan ancestry and their massiveness to their Prejvalsky ancestry and to crossing and selection. Instead of shunning the Oriental ancestry of their stock, breeders of draft horses have reason to point with pride to the way in which builders of their breeds combined the desirable qualities of the two ancient stocks into one harmonious whole. This general tendency of modern breeders and breed promoters to dodge acknowledgment of the crossbred ancestry of most, if not all, of our modern breeds is an unfortunate attitude of mind because it portrays a lack of appreciation of modern biology: it has been clearly demonstrated that the gene remains uncontaminated by its association with other genes, and if any breeder is entitled to be called a master breeder it is the breeder who can mix two or more old groups of genes (races, strains, or breeds) and then bring out new combinations of genes that are an improvement on each of the old.

The belief that our modern horses have been derived from three distinct strains does not preclude belief in a common ancestor; it merely pushes the common ancestor a little further back in history.

It is quite agreed that our present breeds of cattle are derived from two aboriginal races: one large and commonly known as the Urus (*Bos Taurus primigenius*) which stood about six feet high at the shoulders and existed in the early stone age; the other a smaller type commonly known as the Celtic ox (*Bos longifrons*) which also existed in the early stone age. The closest

connecting link we have with these prehistoric forms are the wild White cattle of England.

Swine may be traced to two prehistoric stocks: the wild pig of Europe and the Asiatic pig. By the mixing of these two and their several substrains and through years of selection, breeders have built up our present breeds of swine.

Because not much is known of prehistoric man's association with sheep, little is known of the ancestral type. The Old Testament makes frequent mention of the pastoral occupation of sheep herding, and we may conclude that man valued sheep long before that period. Primitive sheep were undoubtedly a very inferior stock, their wool running strongly to hair, scanty in its covering, and of various colors (Fig. 6).

The Egyptian Age. The first conscious control of animals' parentage undoubtedly marks man's beginnings as an animal breeder. This apparently antedates the time of Prince Mehenwetre of Egypt, who reigned about 2100 B.C. In 1919 a chamber, previously overlooked, in the tomb of this prince was discovered and opened for the first time since it was closed by the Egyptians over 4,000 years before. The chamber contained models of Egyptian life, more nearly perfect than any that had up to that time been discovered. It was the Egyptians' custom to bury with the deceased his tools and weapons; and if he was wealthy they included many additional articles, such as figures of servants at their daily work and miniature models of the many and varied possessions of the deceased. (Many of the early peoples buried servants alive with their masters. At the time of the Spanish invasion of Mexico the Aztecs followed this practice.) In this particular chamber were found models of cattle, barns, a brewery, a bakery, an abattoir, and many illustrations of their daily life.

The largest of these models showed the prince counting his cattle as they passed by. The census, which was found, disclosed that he owned 835 long-horned cattle, 220 polled cattle, 750 donkeys, 974 sheep, and 2,234 goats. Apparently the Egyptians took some note of the arts of animal breeding, as one of the models illustrates the differences in type between the wild animals and the improved ones (Fig. 4). As mentioned above, polled cattle also existed at this early period (Fig. 5), and it is also

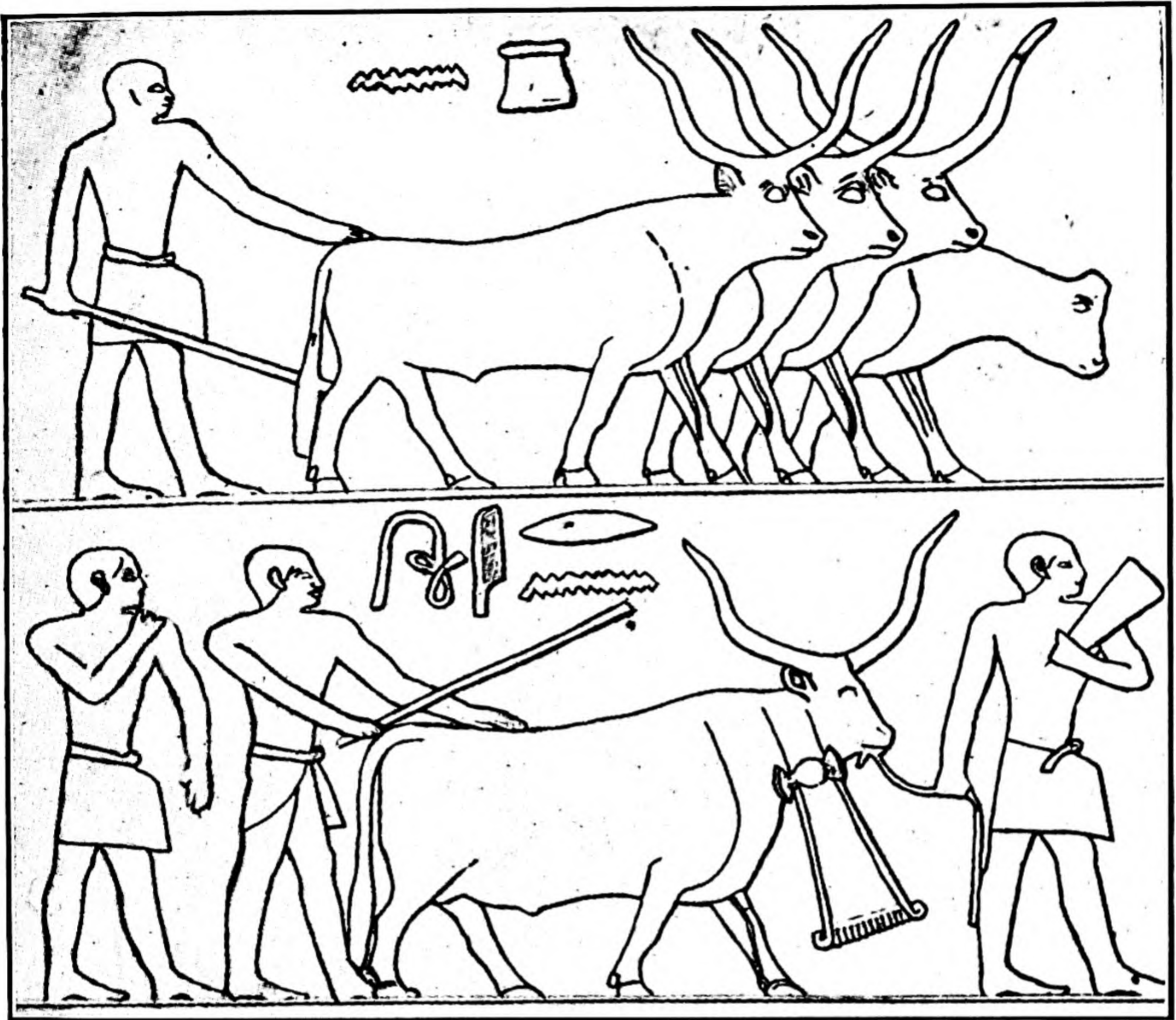


FIG. 4. An Egyptian model illustrating the difference in type between improved and unimproved animals. (Courtesy of the *Field Illustrated*.)

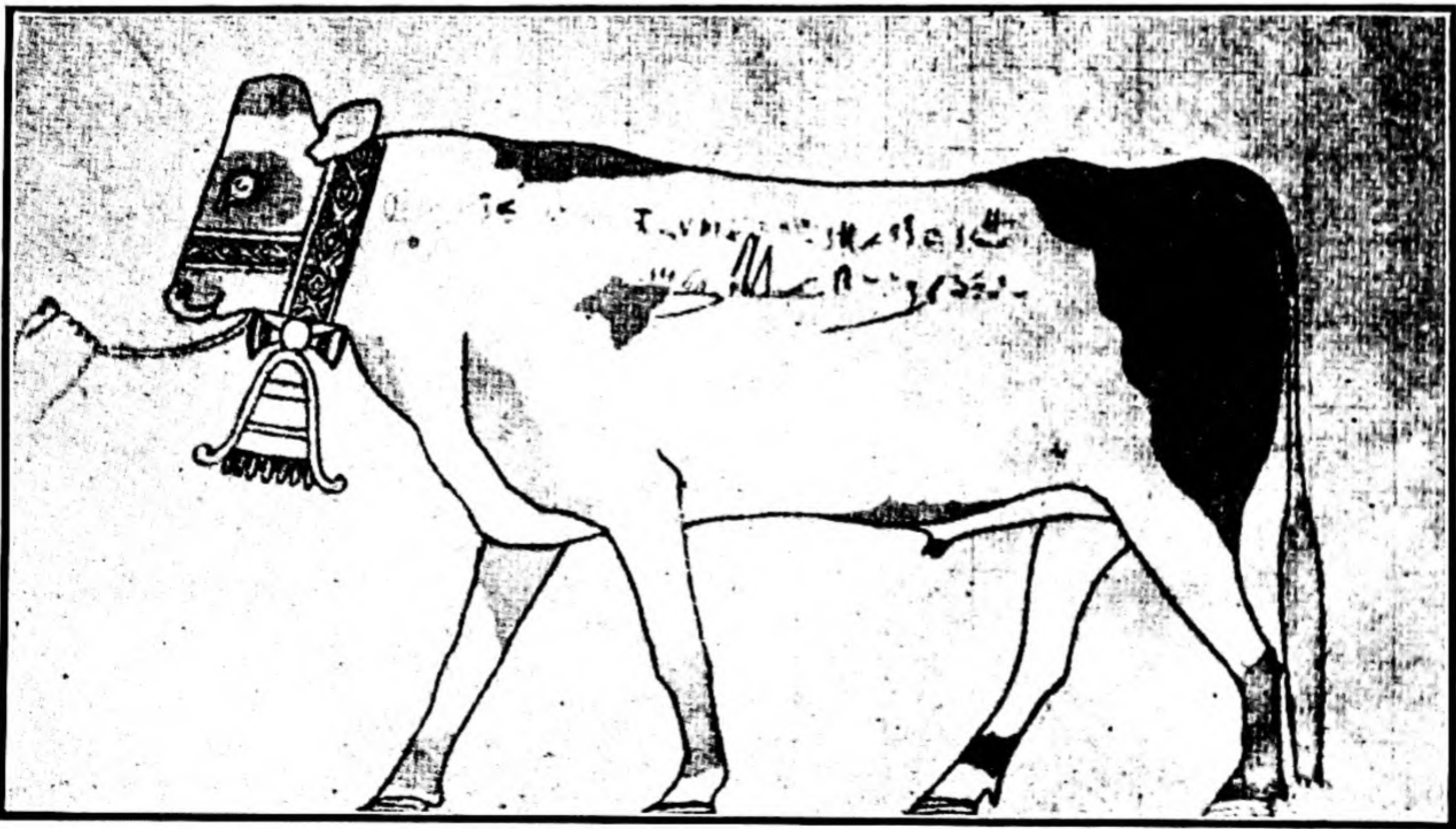


FIG. 5. An Egyptian model of a polled bull. (Courtesy of the *Field Illustrated*.)

quite certain that there were different breeds or types of cattle, each of which had its partisans.

The art of feeding is seemingly also an old art, for one of the models illustrates cattle in the process of being fattened. Furthermore, the art of curing meat is apparently an old one, for the model illustrating an abattoir shows meat being hung up to dry. The tomb of Tutankhamen, opened in 1923, contained large quantities of cured meat in a perfect state of preservation after having been sealed for approximately 3,000 years.

On the whole there is no reason to believe, however, that the Egyptians knew anything of the science of animal breeding, or that during their long period of civilization they accomplished much more than a crude beginning in the art of animal breeding.

The Other Ancients. Much has been said and written of how much early peoples, especially the Bedouin Arabs, knew about and accomplished in the practice of animal breeding. Neither Ridgeway (1905) nor Daubeney (1857) gives much credence to the idea, for according to them the Arabs did not know the first principles of horse breeding. The Arabs considered the dam the all-important factor in the breeding of superior horses; they would never sell a good mare but it was easy to purchase their best stallions. Ridgeway rejects the theory that the Arabian horse was an artificial product of the Arab people and states that the Arabs did not begin to breed horses until between the first and sixth centuries of the Christian era. He considers, and gives much evidence to support his contentions, that the Arab secured his best horses from the Egyptian, that the Egyptian in turn secured his from the Libyan, and that the Libyan inherited them as an indigenous breed of North Africa.

It is very likely that none of these early peoples was as efficient in either the art or the practical understanding of animal breeding as they have often been described. The Greeks and the Romans left written documents from which we may judge their understanding of the subject. Daubeney (1857), in a review of the writings of the Roman Columella, states:

Broodmares were frequently kept in large troops, which were removed, according to the season, from the mountains to the coast, and studiously kept apart from the males, except in the breeding season, when in Columella's opinion, it was more expedient to bring them to-

gether, because the mares, if debarred at that period from sexual intercourse, are apt to conceive by the winds, and in that case to engender an offspring which is sure to die within three years.

Aristotle apparently had very similar views regarding reproduction and inheritance. The following are taken from the writings of Aristotle as translated by Cresswell (1902): "The pregnancy and conception of barren eggs is quick in most birds, as in the partridge, on account of the violence of their sexual desires; for if the hen stands in the way of the breath of the male, she conceives, and immediately becomes of no use for fowling . . ." "Sheep become pregnant after three or four acts of sexual intercourse. If rain falls after the act of intercourse, it must be repeated." Regarding color inheritance he states, "The lambs are white or black according as the veins beneath the tongue of the ram are white or black."

From these and many other documents written in similar vein it is certain that neither the Greeks nor the Romans had much conception of the problem of livestock improvement. Nevertheless, some improvement was made. Aristotle at least made many important observations and, although from many of these he drew faulty conclusions, he at least opened the whole subject of biology.

Both the Greeks and the Romans raised horses, asses, cattle, swine, sheep, goats, fowl, geese, ducks, guinea hens, and pigeons. The Romans introduced improved sheep into Spain, and Caesar is reputed to have taken special note of the horses and horsemen of Flanders.

Some progress was made in the development of what may be called standards of perfection, for Daubeney (1857) quotes Columella as follows:

The oxen we buy should be young, square, with large members and lofty horns, black and strong; the forehead broad and rough; the ears hairy; lips and eyes black; noses flat and turned up, with wide nostrils; a long and brawny neck; dewlaps large, and reaching down to their knees; chest broad, shoulders large; belly protuberant, with sides well stretched out; flanks broad; back straight and even, or a little declining; hips round; legs compact and straight, but rather short; knee-joints well set; hoofs large; tails very long and hairy; hair over the whole body, thick and short, either red or a dark brown; and the coat altogether very soft to the touch.

With regard to the bull, the chief differences from the above are, he is fierce-looking, more lively in his deportment, with a neck more brawny, and so large indeed as to form a large part of his body; and a belly a little smaller in its dimensions than is suitable for an ox.

The cow on the contrary, most to be approved of, is of a tall make, long, with a very large belly, a very broad forehead, eyes black and opening widely; horns graceful, smooth, and black; hairy ears, very large dewlaps and tail, hoofs and legs of moderate size.

Some improvement in animals was undoubtedly made during the periods of these two great empires, but the change apparently was but slightly different or more rapid than that occurring under natural selection.

British Royalty. British royalty at an early date became interested in the improvement of horses. At first the improvement was directed toward developing a better war horse and later toward the development of a race horse. King John imported 100 stallions from Flanders early in the thirteenth century, and in the fourteenth century Edward III imported about 50 Spanish horses at a great cost. Henry VIII, even with all his other activities, found time for horse breeding. He maintained a royal stud, imported horses from Turkey, Spain, and Italy, and had laws enacted regarding horse breeding. The prevailing horses of that period were, however, relatively heavy. Horses were bred primarily for army use and, as at that time not only the men but also the horses were covered with armor plate, only a heavy horse could carry the weight of a heavy man plus all this armor.

During Queen Elizabeth's reign armor became less popular because it was discovered that speed gave more protection than heavy plate armor. James I, who succeeded Elizabeth, was more interested than his predecessors in sports. He established the race course and a code of regulations for it. He gave considerable attention to the breeding of race horses and imported a high-priced Arabian stallion. All subsequent British monarchs followed James I's lead, patronized the race course, and promoted horse breeding. The chief result was that the stimulant was provided for the breeding of horses on the basis of performance on the race course. It is rather odd that the first really serious efforts at constructive livestock breeding should have been centered around breeding for performance, whereas now, 2½

centuries later, we are in the process of developing performance records to guide us in our breeding programs. It seems odd also that the first serious attempt at improvement was made for sport.

The English Earls and Dukes. While the kings played "the Sport of Kings," the earls and dukes of Northumberland and Yorkshire gave attention to the improvement of their cattle. They imported bulls from Holland for breeding with their native stock. Dutch cattle were also introduced into Herefordshire and undoubtedly played an important role in establishing the foundation for the Hereford breed of cattle.

From the above it may be inferred that the Dutch had already at this early date made considerable progress in improving their cattle. It is also clear, from the history of cattle improvement in England, that after the cross of native and Dutch cattle the British cattle were improved far beyond the best of either of the parental strains and at a more rapid rate than previously. It may be inferred that the recombination of genes made possible by crossbreeding and subsequent breeding from within made it possible for the breeders, through more vigorous selection for useful characters, to develop strains that were distinct improvements over the old strains.

Bakewell and His Contemporaries. The foregoing was merely the prelude to the main event which was ushered in by Robert Bakewell and his contemporaries, chiefly the Tompkins' and the Galliers'. Bakewell was born in 1726 at Dishly Grange, Leicestershire, England, and died in 1795. He was fortunate in having a father who taught him much of livestock husbandry. The same is true of the Tompkins and the Galliers families. Bakewell traveled extensively for his time both in England and on the Continent in quest of superior breeding stock. It is interesting that two centers of livestock improvement should have developed almost simultaneously so far apart, for that time, as Leicestershire and Herefordshire and with distinctly different strains. At a slightly later date still other centers of improvement were developed. Some other force may have been responsible for this almost spontaneous interest in livestock improvement.

The Industrial Revolution and Livestock Improvement. The year 1760 is generally accepted as marking the beginning of Bakewell's constructive work. This was an important year in

human events, for it is also generally accepted as marking the beginning of the Industrial Revolution. The Industrial Revolution extended over a long period of time; it is still in progress and recently has been moving at a more rapid rate than during any previous period of history. The development of machinery was responsible for the Industrial Revolution. The cities were, thereby, industrialized. Up to this time each family, or at least each estate, was a rather complete economic unit; household articles, wearing apparel, and food products were produced and manufactured or refined largely within the confines of each household. There was, of course, a certain amount of trade: those residing in the cities had need to purchase food and other products, and the rural population purchased certain luxuries from peddlers and from the city shops. Since each rural unit was mostly self-sustaining, the large estates had a distinct advantage over the smaller ones, for more specialization was possible.

With the advent of the Industrial Revolution, crafts and trades sprang into existence. Men moved from the country to the city and came to earn their livelihood from the crafts and trades. The migration from the country to the city created a demand for agricultural products. Bakewell saw the origin of a demand for livestock products and set about developing farm animals that were better suited to satisfy the demand.

Bakewell's Methods. Unfortunately we do not have a complete record of Bakewell's methods of procedure, a statement that can be made with equal correctness for many others since Bakewell's time. Housman (1894), one of Bakewell's admirers, stated: "Had he been a man of higher education, we should have been the richer, no doubt, by his contributions to the literature of agriculture. But like other men of his educational level, he was more apt to act well than to tell clearly how he acted. Then he was, perhaps wisely, silent. Yet others gleaned, and indirectly told, the secrets he was accused of studiously concealing."

As one reviews the accounts of Bakewell's work, thus far removed, it appears that the stories of his working in secret and refusing to divulge his secrets are products of the imagination of his contemporaries, largely because they were unable to understand what he was doing. The constructive breeders of today are confronted with the same problem of making the public un-

derstand their methods and the philosophy behind them. Bakewell's two rather pointed remarks which he often used in answer to questions regarding methods, were "Like begets like" and "Breed the best to the best." In those two brief statements, Bakewell undoubtedly had condensed about all that he could tell of his methods without going into details which his listeners were very likely unable to comprehend. Bakewell himself probably had little comprehension of what was involved in his methods, for this was a century before the time of Mendel and over a century and a half before the time when serious application was made of Mendel's findings.

We can, however, piece together fairly well the general principles governing Bakewell's procedures in breeding. They were:

1. Housman tells us that *economy* was the root of Bakewell's strength; in other words his breeding operations, as well as his many other farm activities, were directed at economy of production. It is known that he made certain records regarding the performance of his animals. Housman states, "There was at Dishly an experiment-sty, where pigs nine at a time in sets of three, were weighed, fed on weighed food, and so forth, the weights duly chalked on a board, and the complete notes finally transferred to Mr. Bakewell's book of experiments and results."

2. Bakewell believed in the utility of form and quality of bone and flesh. He is quoted as stating that it is possible to get beasts to weigh "where you want them to weigh." He sought a relative increase in the more valuable cuts. He maintained skeletons and pickled joints of specimens of the best of the Dishly sheep and cattle in a little museum. In this way he was able to make comparisons of one generation with another.

3. The above as well as the records he maintained on economy of gains is evidence that his axiom "Breed the best to the best" meant something far broader to Bakewell than to most stockmen even of today, for here is the beginning of both sire testing and a record of performance. We may also infer that the axiom "Breed the best to the best" governed Bakewell's introduction of new stock, crossbreeding, and inbreeding. Housman rather discounts the view that Bakewell's early foundations rested on crossbreds. Housman, however, a great admirer of Bakewell, was writing at a time when "purity of the breeds" was at a premium. There is considerable evidence that Bakewell intro-

duced choice specimens from other districts into his flocks and herds and that these animals were tested in crosses. In the light of what is now known of crossbreeding it would indeed be strange if some of these crosses were not highly successful. On the basis of what is recorded regarding Bakewell's efforts toward economy it would be even more strange if Bakewell did not use some of these crossbreds as foundation animals. Furthermore it is quite certain that several stocks were drawn upon in laying the foundation for his new Leicester sheep.

Breeding the best to the best undoubtedly led Bakewell to inbreeding. In the light of present knowledge his broad interpretation of *best* coupled with his sire-testing program were sufficient to safeguard Bakewell against the disasters that less able stockmen have encountered with inbreeding.

4. It is unlikely that Bakewell's other axiom, "Like begets like," had the literal meaning to him that some of his adherents applied to it in later years. Bakewell merely maintained that superior animals were more likely to produce superior offspring than were inferior individuals. In his selection of breeding stock he was, therefore, very critical regarding not only appearance but also performance.

5. Bakewell introduced the system of leasing sires which served a double purpose: (1) it netted him a substantial income: the ram Two Pounder was let one season for 800 guineas in cash for two-thirds of the ram's use; and (2) it also served as a means of testing his sires: the ones that proved best were later used at Dishly.

It, therefore, becomes clear that at this early date Bakewell actually made use of all the tools modern breeders are trying to put in general use. He made a variety of crosses and retained the best for foundation stock. He tested by a system that was more comprehensive than some records of performance tests being advocated today. He developed a sire-testing program. Furthermore, he used inbreeding with a success that few have achieved since his day. There can be no doubt that Bakewell left livestock husbandry much richer because of his work.

Other English Breeders. While Bakewell was achieving fame in Leicestershire the Tompkinses and the Galliers were laying the foundation for the Hereford breed of cattle, and in vari-

ous parts of England there was a general quickening of interest in livestock improvement. Bakewell has been criticized for failing to leave a complete record of his methods, but his contemporaries left even less. (Actually it is remarkable that these early breeders left as much of a record as they did, for they lived in the days of the quill pen and these breeders were outdoor men of action.) It is clear that the early Hereford breeders like Bakewell first introduced some breeding stock from the outside; that they were critics of animal form and thus bred for more meat in the valuable cuts; that they maintained some records on animals' performance; and that they inbred. On inbreeding Miles (1888) quotes Mr. Price, an early Hereford breeder, as follows:

I bought from Mr. Tompkins a considerable number of his cows and heifers, and two more bulls. I have kept the blood of these cattle unadulterated for forty years, and Mr. Tompkins assured me that he had bred the whole of his stock from two heifers and a bull, selected by himself early in life, without any cross of blood.

My herd of cattle has, therefore, been bred in-and-in, as it is termed, for upwards of eighty years, and by far the greater part of it in a direct line, on both sides, from one cow now in calf for the twentieth time. I have bred three calves from her, by two of her sons, one of which is now the largest cow I have, possessing also the best form and constitution; the other two were bulls, and proved of great value, thus showing indisputably that it is *not* requisite to mix the blood of the different kinds of the same race of animals, in order to keep them from degenerating.

The Colling brothers learned their first lessons in livestock improvement from Robert Bakewell. They apparently were able to comprehend Bakewell's teachings for they copied most of his methods: they first combed the country for the best foundation stock available, selected with great care, and used inbreeding to fix characteristics.

Thomas Bates (1775–1849) studied the methods of the Colling brothers. He, like Bakewell, possessed the mind of an investigator. He is reputed to have kept careful records of feed consumption in relation to both beef and milk production. Bates selected with extreme care and inbred very closely. He developed one of the great herds of all time, and it was a highly inbred herd.

Development of the Breeds and the Establishment of Record Books. Breeds as we know them did not always exist. Most, and perhaps all, breeds that have achieved prominence came into existence because of an economic need, or at least a demand, for a certain type or kind of animal. The most progressive farmers set about to produce that kind of animal because of the need and not with the specific idea of producing a new breed of livestock. As an illustration of this point the Colling brothers began laying the foundation for the Shorthorn breed in 1775; Coates published the first Shorthorn Herd Book in 1822.

The same general procedure has been followed in the development of all the breeds and in the work of all the great early breeders. The Hampshire Down breed of sheep was developed in south-central England, and the early improvement was largely due to the work of William Humphrey. According to Plumb (1920), a notable authority on the history of the breeds, two native stocks were first crossed repeatedly. Humphrey started his work about 1834; he selected the best of the native stock and crossed it with both Southdown and Cotswold rams. This was followed by breeding from within. Humphrey was very exacting in his selection of breeding stock; Plumb quotes Hopkins on this point as follows:

Every lamb was marked as it fell, and those which showed any breachiness or coarseness were notched at the top of the ear; and no matter how well these lambs turned out, they were castrated and went to the butcher. . . . The ewes that were thought good enough for the flock were bred from until they were worn out. One favorite was kept till she was fourteen years old, and her last lamb was Oliver Twist. This ewe had no udder for the last four years of her life, and Oliver Twist was given to another ewe. This ram was first in his class at Leeds and Battersea.

The early history of every noted breed follows a similar vein. Herdbooks were established after the breeds were well along in development. Breeds were established in order to obtain a more productive stock, and herdbooks were established to protect the purity of the established strains; each was an important step in the progress of animal breeding.

The Importation of Improved Animals to America. Merino sheep were introduced in the United States as early as 1793, and

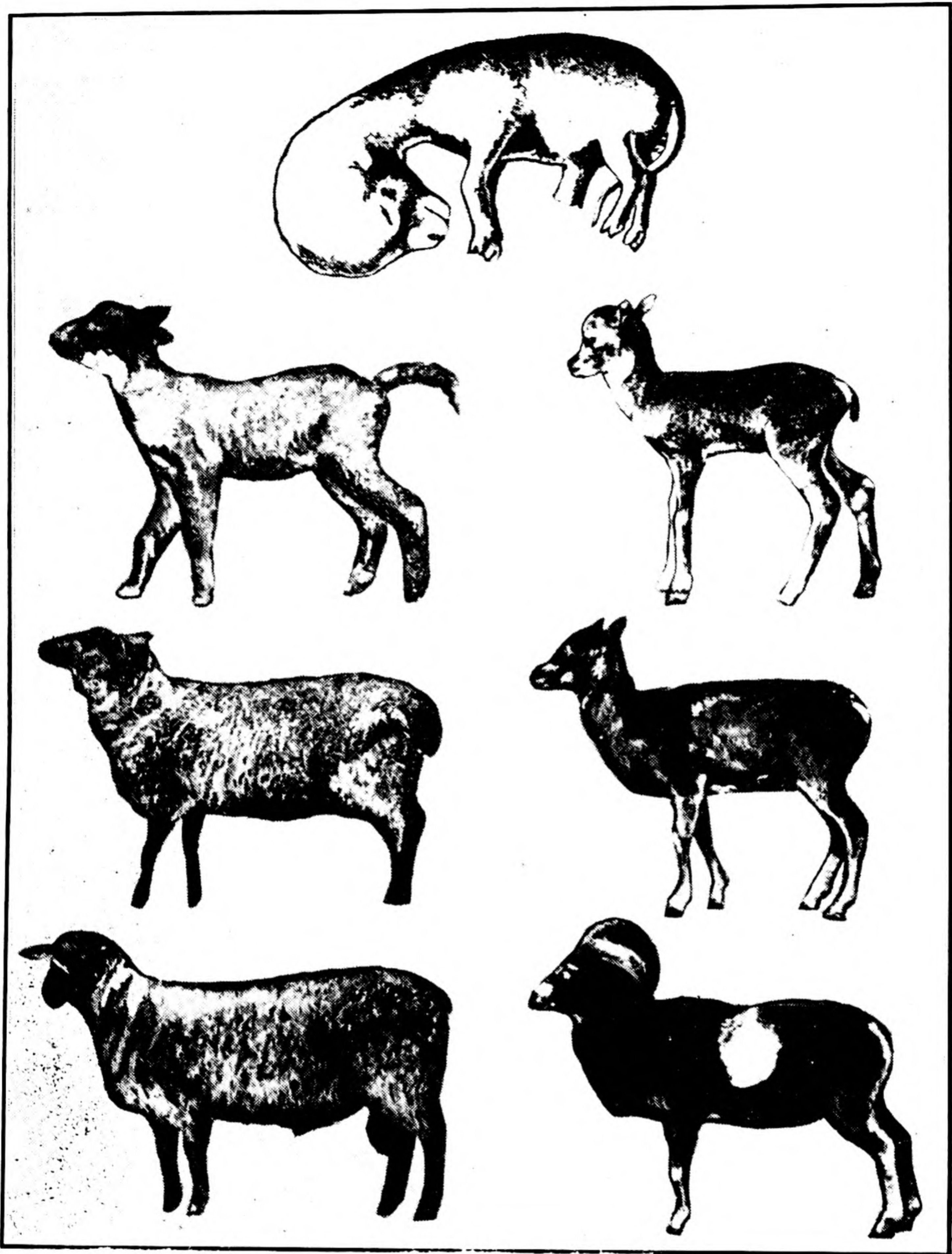


FIG. 6. Illustrating the changes in proportions of the improved Suffolk and unimproved Mouflon breeds of sheep as they grow. To a considerable extent this illustrates the evolution of the sheep through breed development and improvement. (From Hammond, *Farm Animals*.)

Leicester sheep were smuggled into the colonies even before the Revolutionary War. The heavy importation of improved British livestock did not get under way, however, until the rich lands of the Middle West were developed into farms and improved transportation made the marketing of livestock possible.

Breed associations were established in this country shortly after the close of the Civil War. They were established here as abroad for the very worthy purpose of protecting the purity of the strains and of protecting the public from the less scrupulous stock dealer.

Spreading of the Purebreds. The improved stock brought from Europe was so superior to the animals then on American farms that the word "imported" came to have special significance to American stockmen. In like fashion the word "purebred" came to have special significance. As a result, since imported stock and purebreds were scarce, the available animals generally sold at substantial prices. As long as this situation prevailed nearly every animal eligible for registration was registered and sold as a purebred. A degeneration of the merit of many registered animals resulted because culling was practically nonexistent. Furthermore many people developed the misapprehension that purebreds were different from non-purebreds. The term "purebreeding" came into rather widespread use, and gave the impression that purebred animals were genetically pure. The term has been an unfortunate one: first, it is a misnomer, for in the light of modern genetics not many animal breeders have hopes of producing farm animals that are genetically pure even with intensive inbreeding and rigid culling; and second, since in many commodities there is a close relationship between the degree of purity and value, the general public came to associate so-called purebreeding or purebred with merit.

The Purebred Philosophy. For the past sixty years American thought regarding animal breeding has been largely dominated by what may be called the purebred philosophy. This philosophy recognizes differences between individual purebreds, but it holds that the purebred, by virtue of its being a purebred, is superior to animals bred otherwise. This philosophy goes even further and would have other stock replaced by purebreds so far as possible. Harper (1920), when this philosophy had about reached its height, expressed the belief very well as follows:

It is universally accepted, all things considered, that purely bred animals excel grades. For this reason well-bred animals command a fancy price which often prohibits their use; nevertheless, they have a number of very strong advantages over grades, chief of which are their capability of higher production, their stimulating effect upon the breeder, thus favoring general improvement, and the increased value of their offspring. These advantages are often sufficient to offset the high price.

It will be shown later that this philosophy is far from being compatible with present known facts regarding the breeding of improved animals. It should be recognized, however, that this philosophy did serve a purpose and that progress was made in the improvement of American livestock by following its teachings.

The Livestock Show. The livestock show or fair has played an important part in the development of animal breeding. The modern livestock show is the outgrowth of the old European, British and Continental, markets or fairs held as early as the Middle Ages. The market was a place for the exchange of goods, live animals being one of the commodities offered for exchange or sale. Fairs were different from markets because they were held less frequently and they usually included some entertainment. The assembly of a number of animals and their owners and caretakers led to discussions and arguments regarding the animals' respective merits. Arbitrators had to be called to settle disputes, and eventually definite classes were established. The Smithfield Market of London is said to date back to the year 1150; the first Smithfield Fat Stock Show was held in 1799.

The livestock shows have had an influence on livestock improvement and its philosophy. The show like the development of breeds and the establishment of herdbooks has contributed to livestock improvement. Sanders (1914) sums it up well in a quotation from an English Hereford breeder:

I remember once a gentleman who lived seven or eight miles off me, asking if I would come and see a young bull that he thought was a remarkably good one. He desired to know if I would advise sending him to the Ludlow Show a few miles off.

I said, "Certainly, send him." He was an indifferent animal, but I could see that his owner thought him a wonderfully good one, so he sent him. It was a fairly large class, and the bull was not in the first seven noticed by the judges. The owner came to me and said, "You made a mistake in advising me to send the young bull." I told him

that I had made no mistake, that I could see that he had no chance of winning, but that I could also see that he thought his calf a very good one, and having one in the class myself (which took second prize) I felt sure he would think, had he not sent him, that he would have been near winning. He came to me an hour or two afterwards saying, "You have given me the best lesson I ever had in my life, for I did think he would about win until I saw him with the others."



FIG. 7. The Royal Agricultural Society's showyard at Cambridge, 1840.
(From *Jour. Roy. Agric. Soc. of England.*)

The show has stimulated interest in better animals and it has been an important factor in setting ideals. Perhaps the chief criticism of the livestock show is that in recent years, at least, its adherents have come to take it too seriously; it, like the "spreading of the purebreds," came to be an end in itself. Both have been steps along the long path of improvement but they do not mark the end—the end is not yet in sight.

Not All the Emphasis on Show. It is very clear that several of the early breeders gave recognition to performance: Bakewell, the Colling brothers, and Bates all used records of a sort.

In 1882 a list of registered Jerseys that had completed churn tests and had produced 14 or more pounds of butter in 7 consecutive days was made available. In 1884 a volume entitled "Butter Tests of Jerseys," a continuation of the list, was published.

In 1870 the Holstein cow, Dowager, was reported to have produced 12,681 pounds of milk in one year. Five years later the highest production was 16,274 pounds, and in another five years the record was 18,000 pounds.

In 1890 Dr. Babcock had completed perfection of his butter-fat test, and from that time on increased attention has been devoted to records of production in dairy cattle.

Laying trials, first held in England in 1897, were apparently the first organized effort to stimulate interest in identifying superior laying stocks. In Canada and the United States the first egg-laying contests were held in 1911, the former in British Columbia and the latter in Connecticut.

Out of such beginnings have grown record-of-performance tests for both dairy cattle and poultry, and each year record productions have been pushed higher and higher. Unfortunately, however, too little of the benefit has radiated out to the rank and file of our herds and flocks. It is estimated that after all the effort that has been put into cow testing only 5.1 per cent of the milk cows in this country are tested.

The difficulty may be that the wrong approach has been made to the spreading of improved germ plasm. Perhaps, instead of attempting to get a high percentage of the commercial stock tested, tests and purification of the key herds and flocks should be emphasized, with the expectation that the benefits would radiate to the commercial producer. We have observed this procedure to be successful in crops.

There can be no doubt that both the breeder and the commercial producer of today are interested in efficiency of production. Here lies a great opportunity for improvement of the economic position of the livestock industry. The problem is to organize the industry so that present knowledge of animal improvement may be used to full advantage.

BIOLOGY IN RETROSPECT

Studies by Aristotle (384–322 B.C.) are generally recognized as marking the beginning of the development of biological science. In 1675 Hamm and Leeuwenhoek discovered the human sperm, in 1672 De Graaf discovered the Graafian follicle, and early in the eighteenth century Spallanzani showed that both sperm

and eggs were necessary for the initiation of development. The great significance of these fundamental facts on animal breeding remained unrecognized until after the rediscovery (1900) of Mendel's laws.

Many notable contributions were made, however, to biological science during the eighteenth and nineteenth centuries. These contributions eventually helped to clarify genetic knowledge, but many of them clouded the issues for the time being. Darwin's (1859) great contribution, "Origin of Species," led to a great deal of confused thinking regarding genetics. During the latter portion of the nineteenth century and early in the twentieth century, animal breeders and many biologists were chiefly concerned with the inheritance of acquired characters, telegony, and maternal impressions; Manly Miles (1888), one of the most progressive educators of his day on livestock breeding, wrote

The habits and characteristics of animals that have been developed by the conditions in which they are placed, or the peculiar training they have received at the hands of man, appear to be transmitted from generation to generation, with nearly the same certainty and uniformity as those that characterize the original type or species from which they are descended. . . . The influence of the male in the process of procreation is not limited to his immediate offspring, but extends also, through the female that he has impregnated, to her offspring by another male.

These beliefs became so well entrenched in the public mind that it was not until about the twenties that they became fairly well uprooted from the minds of even the better informed. Biologists, of course, became aware of the unsoundness of these beliefs at an earlier date. Weismann in the nineties advanced what are still sound arguments against the inheritance of acquired characters. It was not, however, until 1909 that the inheritance of acquired characters was disproved: Castle and Phillips (1911) removed the ovaries from an albino guinea pig and transplanted the ovaries from a black guinea pig in their place; the white guinea pig produced young in accordance with what was expected of a black guinea pig.

In the late nineties Francis Galton, a cousin of Darwin, began to apply statistical analyses to the phenomena of variation and heredity and thus laid the foundation for that branch of biological science now known as *biometry*.

It has been recorded that Bates, while attending Edinburgh University in 1810, learned much of the science of animal breeding which enabled him to achieve still greater success as a breeder when he returned to his farm. At that time there was no biological information that could have aided Bates in furthering his breeding program; at that time, and still later, the leading biologists depreciated inbreeding, the tool that Bates used with such remarkable success.

Mendel. In 1866 the Austrian monk, Gregor Mendel, published results of his studies from the crossing of peas. These results came to be known as Mendel's laws and laid a foundation for that branch of biology known as *genetics*. It would be difficult to make even an estimate of the economic benefits man has already reaped from the applications of these fundamental principles, and it appears today that man has not as yet made even a good start in the application of the principles to increased production of food and clothing.

Rediscovery of Mendel's Laws. Mendel's work was so far ahead of his day that the results remained unheeded until thirty-five years later when they were rediscovered simultaneously by de Vries, Correns, and Tschermak. That the laws were published in an insignificant publication is not sufficient explanation for their being unheeded. Biologists of that period were absorbed with the topics of evolution and the inheritance of acquired characters.

Early Studies of Gene Identification. After the rediscovery of Mendel's laws interest and research in the new field increased rapidly. At first it appeared that it would be very simple to breed better plants and animals with the aid of these new biological principles. As investigators proceeded with their researches, they found that what they had come to think of as characters were not inherited in the simple Mendelian pattern. Plant breeders went much farther with gene identification than animal breeders and have succeeded in making some applications to practical breeding from these studies. Researchers in the animal field have contributed little directly to the job of breeding better animals through this method of attack. They have, however, helped to demonstrate that few characters of economic importance are inherited in simple Mendelian fashion, and thus they have aided in building a better philosophy of methods of

improving animals by breeding than was possible early in the twentieth century.

Early Studies of Inbreeding. Significant studies of inbreeding were reported by East on corn in 1907, by King on rats in 1918, and by Wright on guinea pigs in 1922. These and other studies laid a foundation that changed the whole philosophy of the applications of Mendel's laws to the improvement of plants and animals. Plant breeders were quick to make practical use of these facts, and by 1930 plant breeding was being advanced rapidly.

Early Studies of Inbreeding Farm Animals. During the twenties several experiments of inbreeding farm animals were initiated. Taken as a whole, these studies yielded negative results, but they were at least useful in demonstrating how not to proceed with inbreeding farm animals. As seen in retrospect, these early attempts at inbreeding farm animals were, for the most part, weak in four respects: (1) the best stock available was not used as a foundation; (2) selections were not made on the basis of performance; (3) rigid systems of breeding, full brother-sister matings for example, were followed; (4) the experiments were conducted on too small a scale.

Studies of Crossbreeding. During the thirties several studies of breed crosses were published. These studies verified what many practical livestock men in Britain and America had for years both believed and practiced. They demonstrated, if there was any cause for doubt on that score, that the livestock breeders through development had made a definite practical contribution to improvement by breeding. The very fact that crossing the breeds usually results in increased vigor is evidence that the breeds differ genetically, and this difference proves that breeders had made progress in the separation of genetic materials. A further benefit from these studies is that they made a definite contribution to the development of systems of breeding.

Records of Performance. Breeders of race horses, dairy cattle, and poultry had, for a long time, given attention to records of performance, but during the thirties several studies and proposals were advanced in regard to records of performance for meat animals. During this time the earlier proposals for dairy cattle and poultry were reworked and reappraised. These studies and proposals also advanced systematic breeding.

Inbreeding. Large-scale studies of inbreeding were initiated during the late thirties and early forties. Most of these studies were centered in the Bureaus of Animal Industry and Dairy Industry of the United States Department of Agriculture, in cooperation with state agricultural experiment stations. These large coordinated studies now cover swine, sheep, poultry, beef cattle, and dairy cattle. A large number of scientific papers have been published as a result of these researches, and several inbred lines of livestock that appear very promising have been developed and released. In the main, the coordinated programs referred to center around the application of inbreeding, crossbreeding, and selection to the improvement of farm animals by breeding.

CHAPTER III

The Reproductive Organs

The process by which new individuals come into being is known as reproduction. Reproduction is an orderly, systematic process by which each of the parents makes very definite contributions to the new individual's constitution. It is through the understanding of this process and its application to the problems of animal breeding that animal breeding is gradually becoming converted from an art to a science.

Birth is commonly considered as marking the beginning

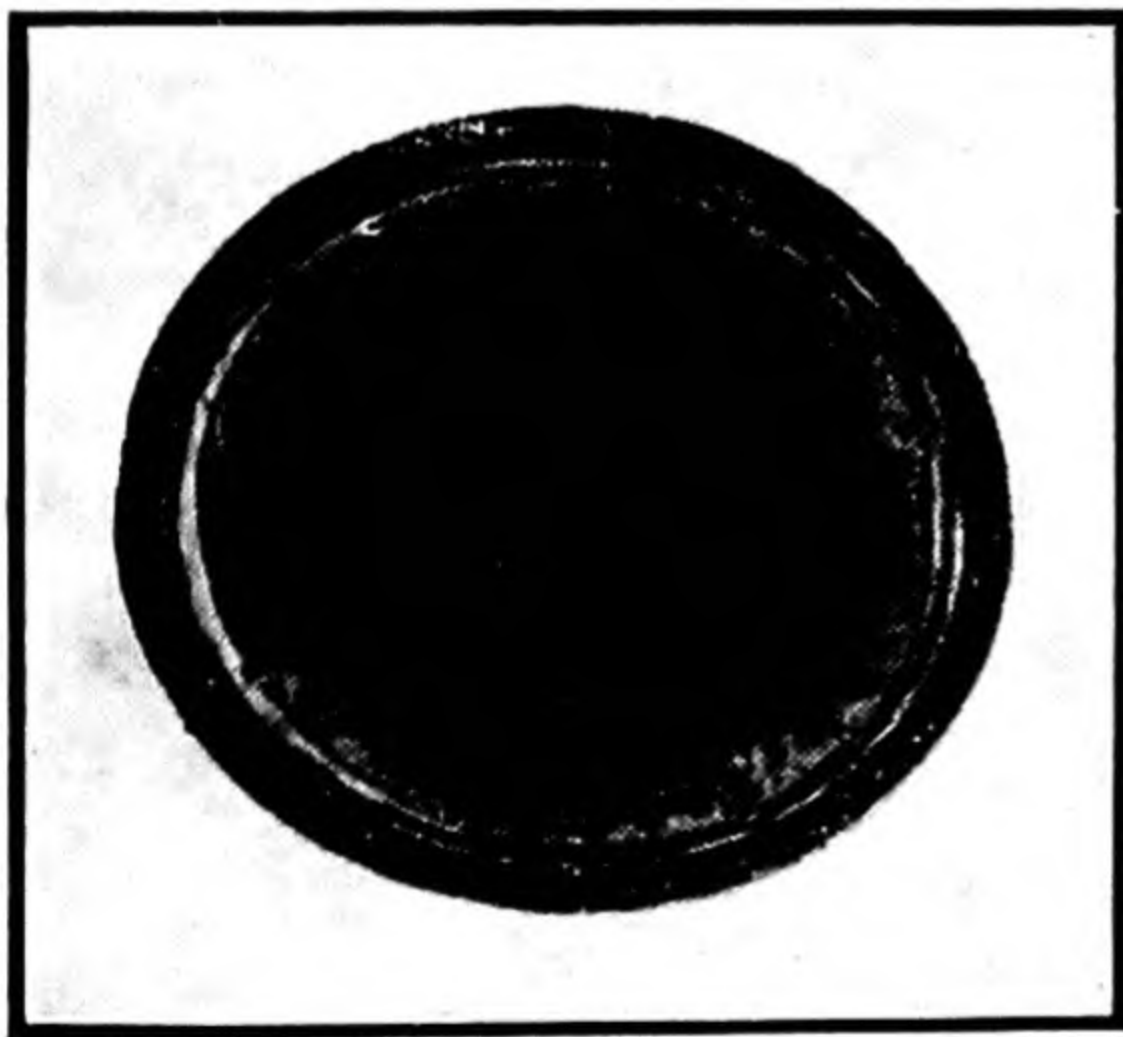


FIG. 8. Ovum from the cow.

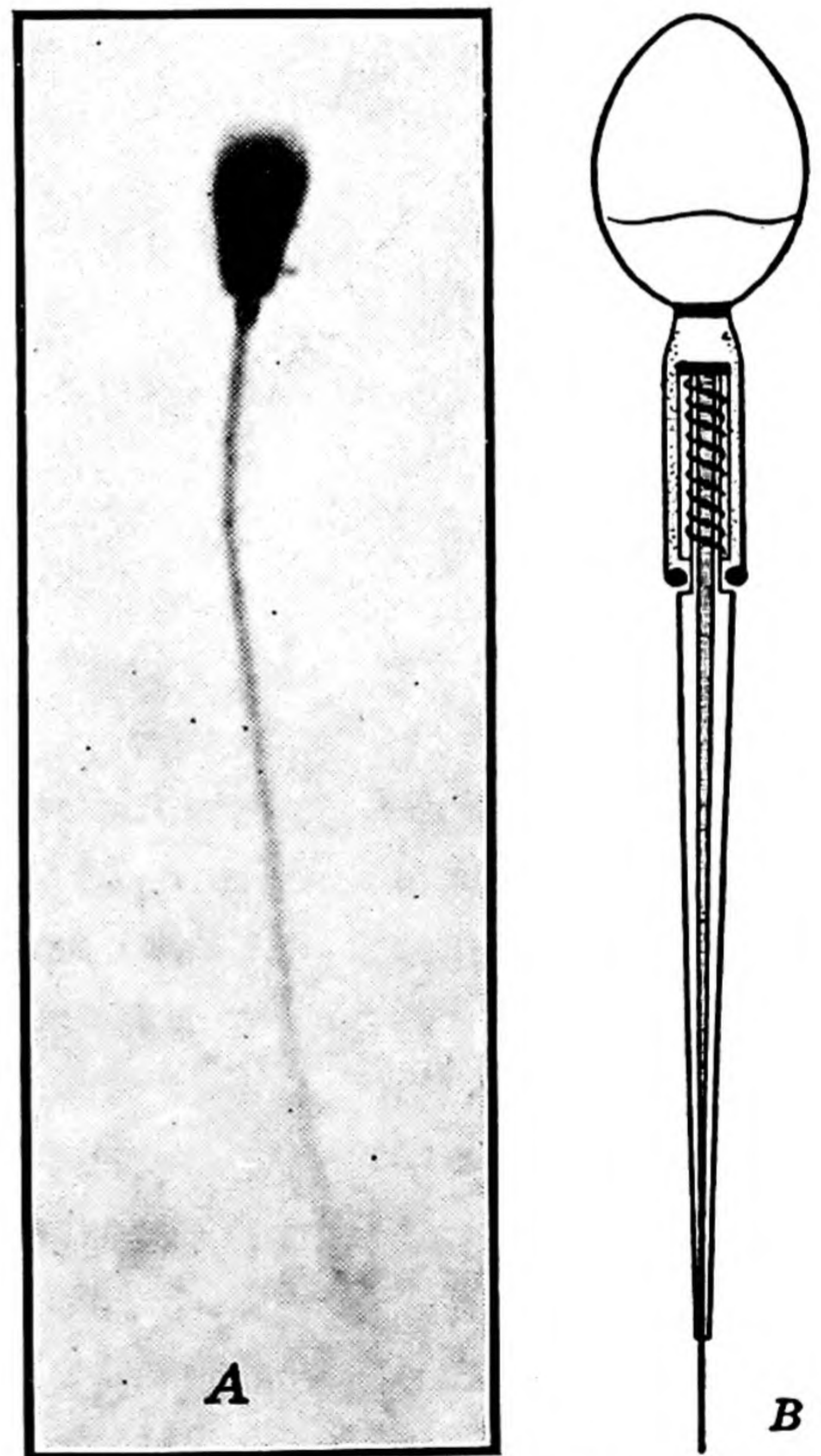


FIG. 9. Sperm cell. (A) Photograph. (B) Drawing. (After Meves, from Arey, *Development of Anatomy*.)

of the new individual's life. Actually the new individual starts its life at the time of fertilization or conception. At this time two germ cells, the egg (Fig. 8) and the sperm (Fig. 9), unite, and thereby the new individual comes into being.

GENITAL ORGANS OF THE MALE

The male reproductive system comprises the following organs: (1) two testes, (2) the epididymides, (3) the *ductus deferentes* (the sperm ducts), (4) the *vesiculae seminales*, (5) the prostate, (6) the two bulbo-urethral (Cowper's) glands, (7) the urethra, and (8) the penis.

The Testes. The function of the testes is to produce spermatozoa. They are enclosed in the scrotum, a diverticulum of the abdomen. At one time the scrotum was considered merely a bag

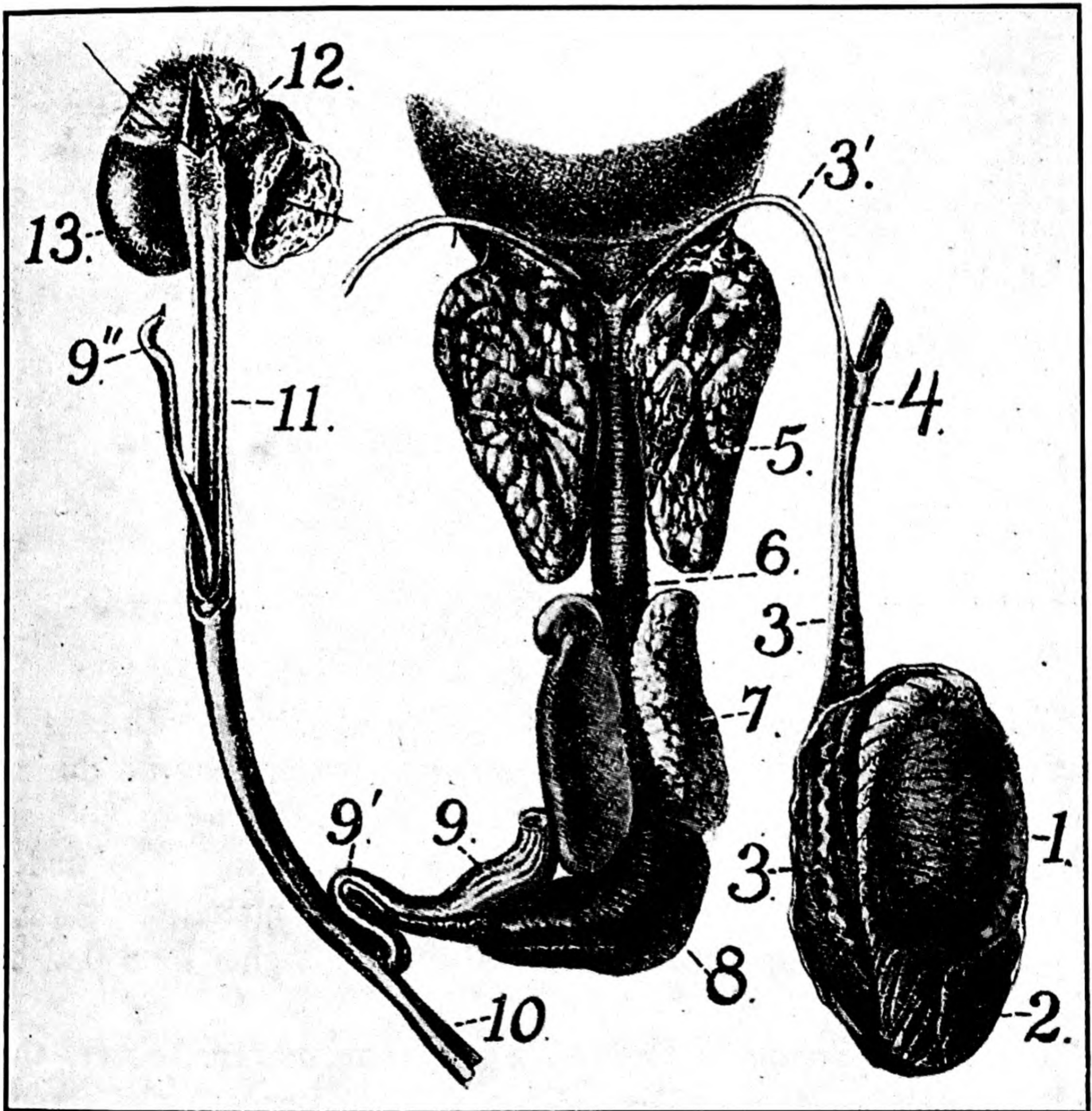


FIG. 10. Genital organs of the boar. (From Ellenberger-Leisering, *Atlas of Anatomy*, Alexander Eger, publisher; reprinted by permission.)

1, Testis; 2, epididymis; 3, vas deferens; 4, artery; 5, vesiculae seminales; 6, prostate; 7, Cowper's gland; 8, muscle; 9, 9', and 9'', penis; 10, retractor penis muscle; 11, prepuce; 12, orifice of preputial pouch; 13, glans penis.

for the testicles. It is now known that in many animals it performs an important task as a thermal regulator. In hot weather or when the animal is heated the scrotum is more pendent, whereas in cool weather it is drawn more tightly to the body. Temperatures only slightly above normal scrotal temperature are highly destructive both to the germinal epithelium of the testis

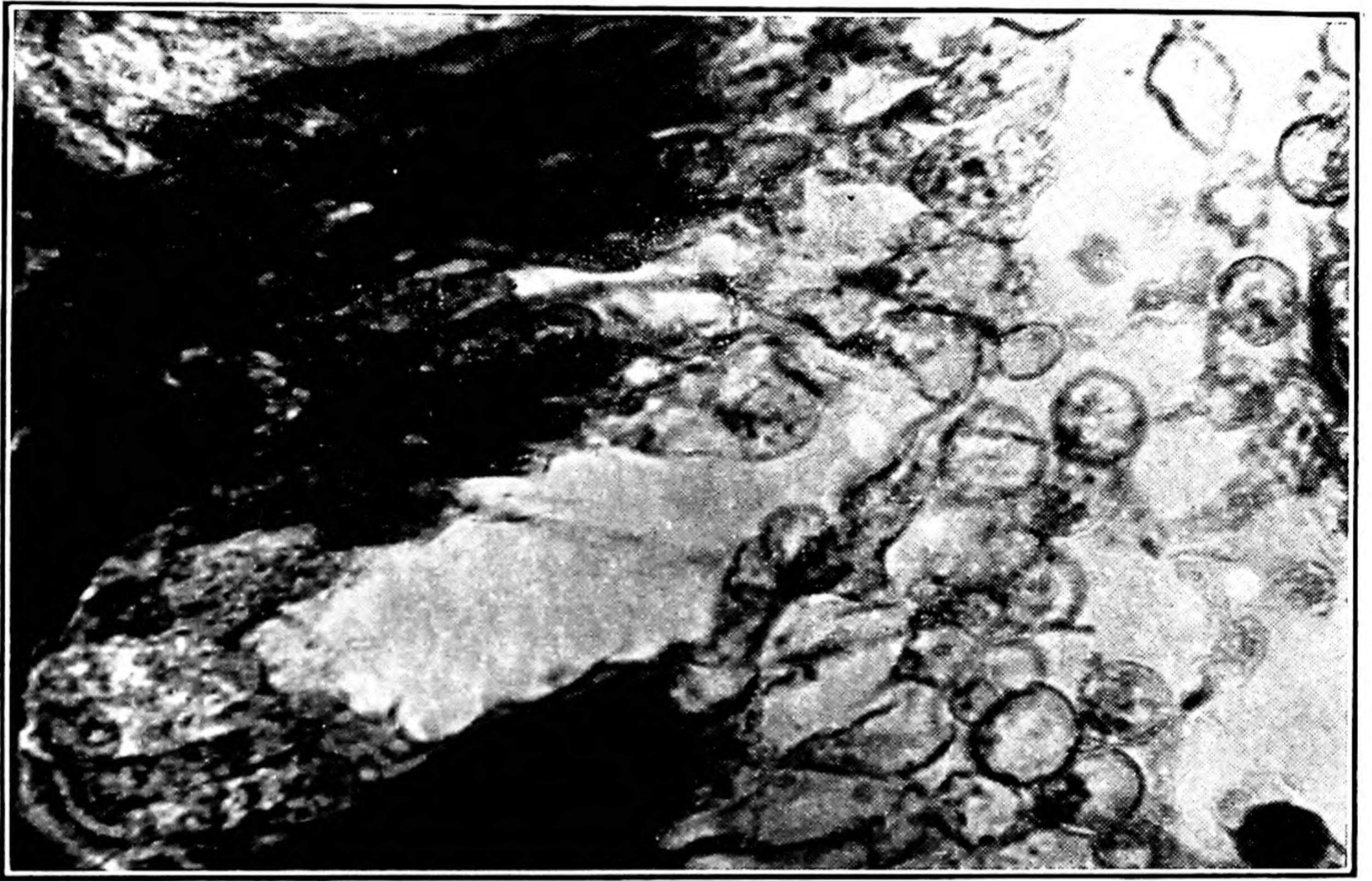


FIG. 11. A section of the efferent duct in the rat, illustrating the pronounced secretory activity of the duct.

and to the male germ cells of many animals. Rams with considerable wool over the scrotum frequently become sterile during hot weather. Cryptorchids are males in which one or both of the testicles have not descended to the scrotum. The undescended testicle is usually sterile, and the explanation is that the abdominal temperature is several degrees higher than that of the scrotum.

The *tunica vaginalis propria*, a serous membrane, covers the greater part of the surface of the testis. Beneath the serous membrane is the *tunica albuginea*, a fibrous capsule rich in lymphatics. Septa of connective tissue and muscle fibers pass from the *tunica albuginea* into the testis in the form of a mass of fibrous tissue called mediastinum testis. Other fibrous proc-

esses project inward and divide the glandular portion into lobules.

The glandular portion of the testis is composed of convoluted seminiferous tubules. Spermatogonia (sperm-producing cells) are situated within the seminiferous tubules. Sperm production is discussed on page 59.

Between the tubules is a loose connective tissue containing numerous lymphatics, blood vessels, nerves, and interstitial cells. The interstitial cells apparently produce a hormone which is vital to the function of the other secretory organs of the male reproductive system and to the sexual impulse. More details of this hormone are discussed under the sex hormones.

Several seminiferous tubules unite to form a straight tubule which passes into the body of the mediastinum. The straight tubules, when within the mediastinum, unite to form a network of vessels called the *rete testis*. The efferent ducts carry the sperm cells from the rete testis to the head of the epididymis. The efferent ducts vary in number (a dozen or more) in different animals. They are lined with epithelium in which the secretory function is highly developed. It is highly probable that this secretion and the secretion of the epididymis contain elements which are vital to the nutrition and ripening of the sperm cells.

The Epididymis. The epididymis is attached to the testis by connective tissue, the efferent ducts, and the serous membrane. It is so closely attached to the testis that it is frequently thought of as part of the testis; it is removed with the testis in castration. It is, however, a distinct organ and has a special function: storage of sperm. It consists of three parts: head, body, and tail. The efferent ducts lead to the head which consists of a dozen or more tubules. These are grouped into lobules (four or five tubules in a lobule) which unite to form a single tube. The single tubes of the several lobules unite to form the single tube or duct of the epididymis. The epididymis proper is a single tube very much coiled; in man it is about 20 feet in length.

The epithelial cells lining the head are columnar and possess marked secretory activity. The body and tail of the epididymis is a storage place for sperm cells. There is some evidence to indicate that sperm cells go through a beneficial ripening process while being stored in the epididymis. The tail of the epididymis leads to the *ductus deferens*.

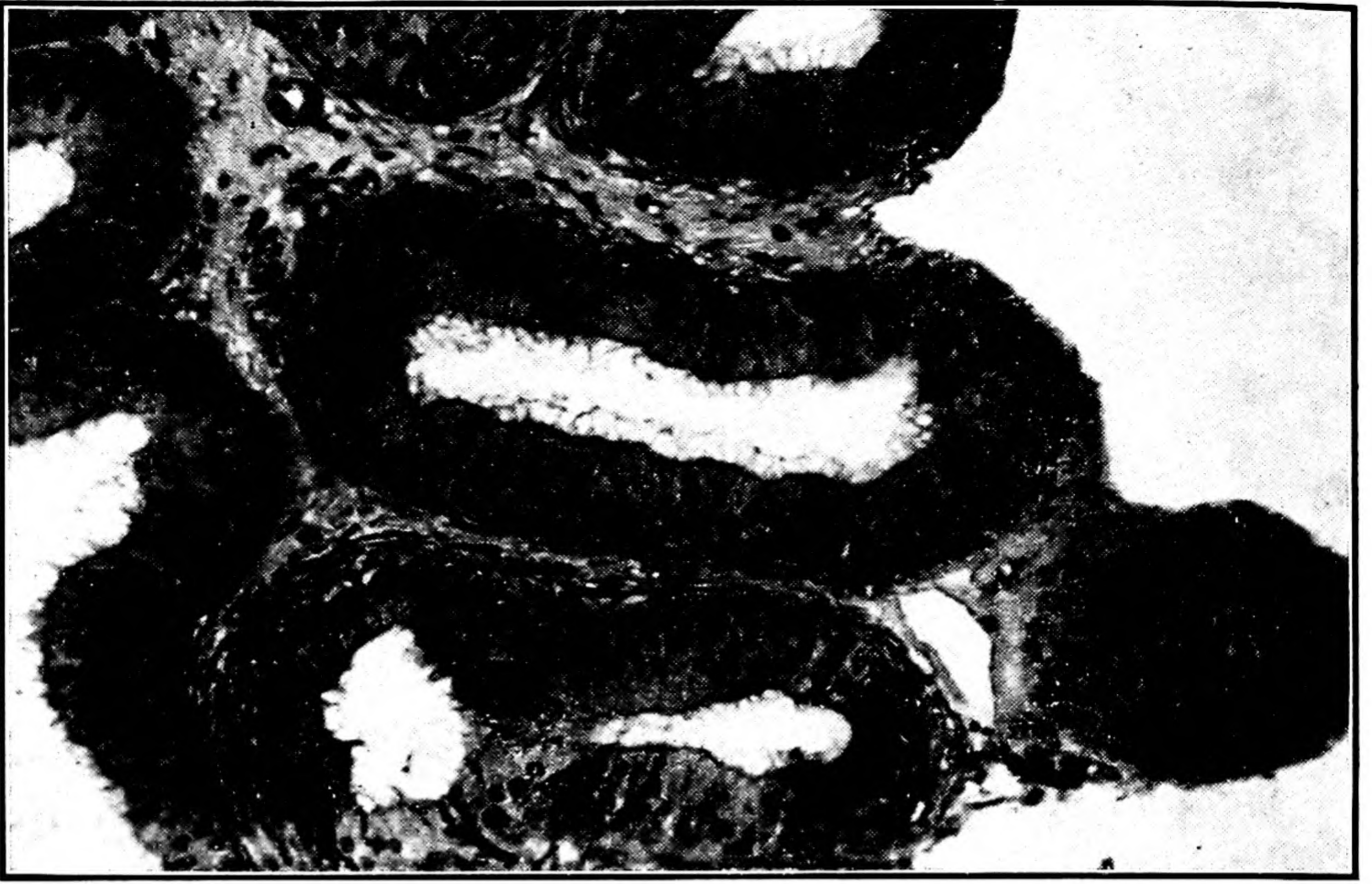


FIG. 12. A cross section of the epididymis showing several tubules.

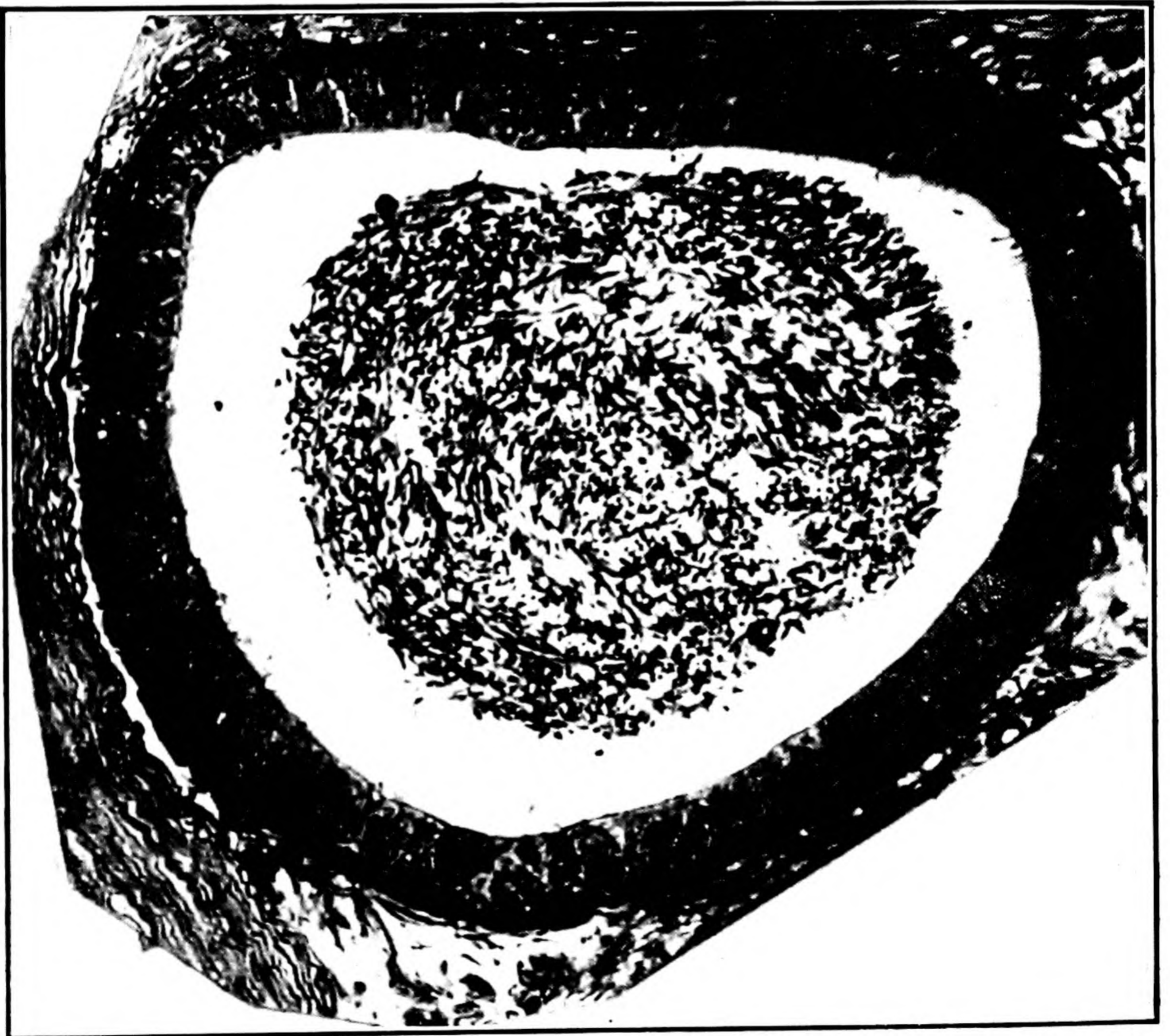


FIG. 13. A section through the body of the epididymis (rat). Note the low epithelium, the small amount of secretion, and the abundance of sperm cells.

The *Ductus Deferens*. This slender tube leads from the tail of the epididymis to the pelvic part of the urethra. The lumen of this duct is very small but the wall is thick and cordlike. Each *ductus deferens* ascends in its inguinal canal and enters the pelvic cavity. The two ducts come to lie close together over the neck of the bladder. Here they are flanked laterally by the *vesiculae seminales*. At this point the ducts enlarge somewhat and are known as the ampullae. The ducts pass under the prostate and terminate in the urethra.

The *Vesiculae Seminales*. This pair of glands flanks the *ductus deferentes* laterally near their point of termination. In the stallion they are 6 to 8 inches long and about 2 inches in diameter. In the bull they are about 4 or 5 inches long and 2 inches in width. In the boar they are very large in proportion to body size, being about 6 inches long and 2 or 3 inches wide.

In the horse the *vesiculae seminales* are bladderlike sacs, whereas in the bull they are compact glandular organs. They open to the urethra at about the same point as the *ductus deferentes*.

The Prostate. This gland lies on the neck of the bladder, at the beginning of the urethra and ventral to the rectum. It is enclosed in a capsule of fibrous tissue, and the glandular portion is divided into lobules. Each lobule is crossed by a duct which gives off numerous branches. The secretion of the prostate is milky in appearance and has a characteristic odor. In old animals the prostate is frequently diseased owing mainly to the presence of calcareous concretions.

The Bulbo-Urethral Glands. These glands, two in number, are situated on either side of the urethra close to the ischial arch. In the stallion they are about 2 inches long and 1 inch wide. They are smaller in the bull and are deeply imbedded in muscular tissue. They are very large in the boar, being about 5 inches long and an inch or more in width.

The Urethra. The urethra of the male is a long tube of mucous membrane extending from the bladder to the *glans penis*. The mucous membrane contains fine elastic fibers and is surrounded by muscular and erectile tissue. The *ductus deferentes* and *vesiculae seminales* open to the urethra close to its point of origin. The urethra, therefore, serves as a passage for both urine and semen. Since urine is toxic to sperm, it has been

assumed that at least one function of the accessory sexual glands (bulbo-urethral, prostate, and *vesiculae seminales*) is to cleanse the urethra and change the chemical reaction within it.

The Penis. This is the male organ of copulation. Its shape and size are quite variable in different species. It is composed essentially of erectile tissue, and at the time of erection it becomes gorged with blood.

GENITAL ORGANS OF THE FEMALE

The female reproductive organs consist of: (1) the two ovaries, in which the ova arise, (2) the two Fallopian tubes or oviducts which convey the ova to the horns of the uterus, (3) the uterus, wherein the ovum implants and develops, (4) the vagina, an organ of copulation through which the foetus must pass when expelled, and (5) the vulva, the terminal organ of both the genital and urinary systems.

The Ovaries. The ovaries are located in the sublumbar region. They are suspended by the mesovarium. In a mare of medium

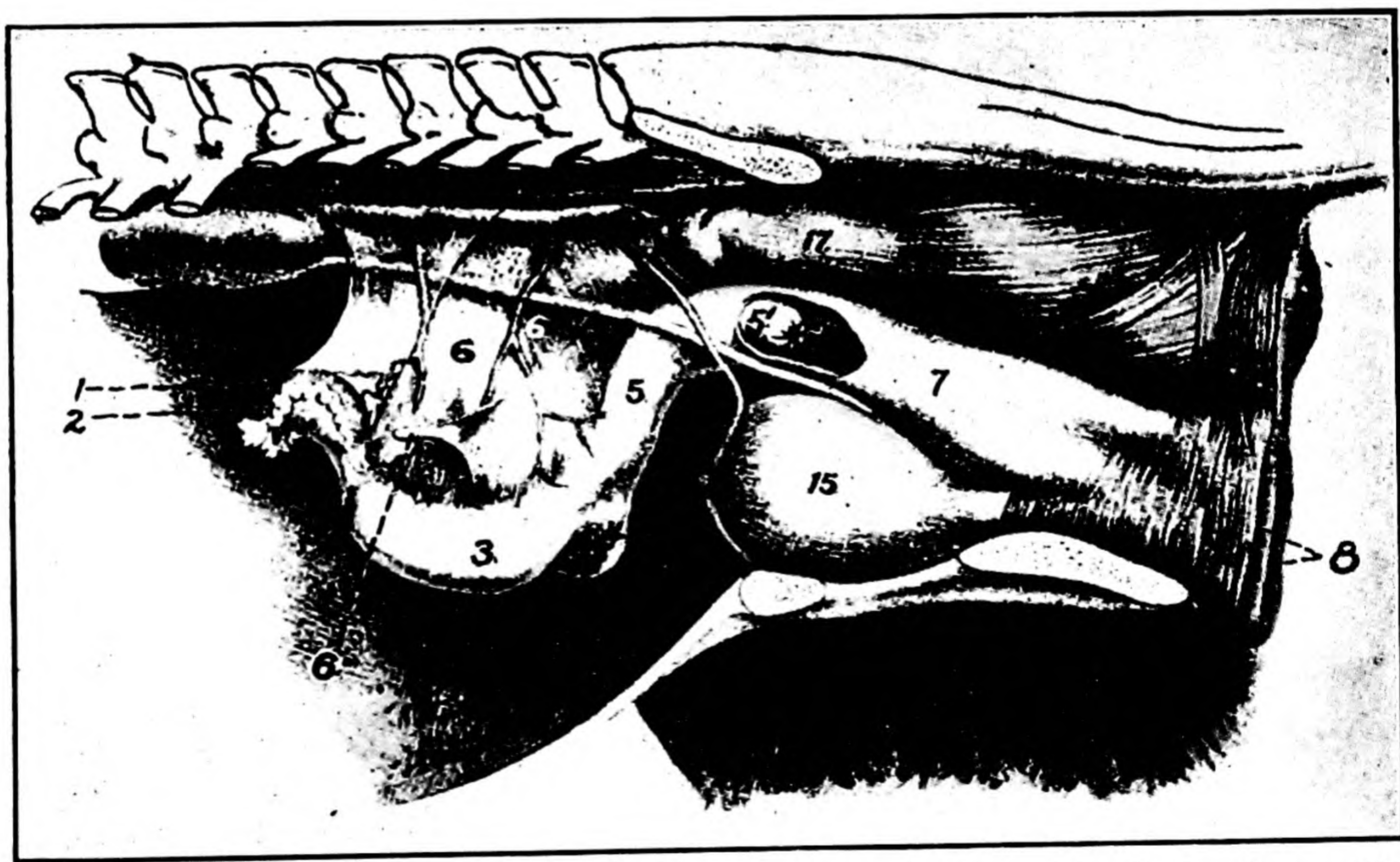


FIG. 14. Genital organs of the mare. (From Ellenberger-Leisering, *Atlas of Anatomy*, Alexander Eger, publisher; reprinted by permission.)

1, Ovary ; 2, Fallopian tube ; 3, left horn of the uterus ; 4, right horn of the uterus ; 5, body of the uterus ; 5' and 5'', os uteri ; 6, broad ligaments ; 7, vagina ; 8, vulva ; 15, bladder ; 17, rectum.

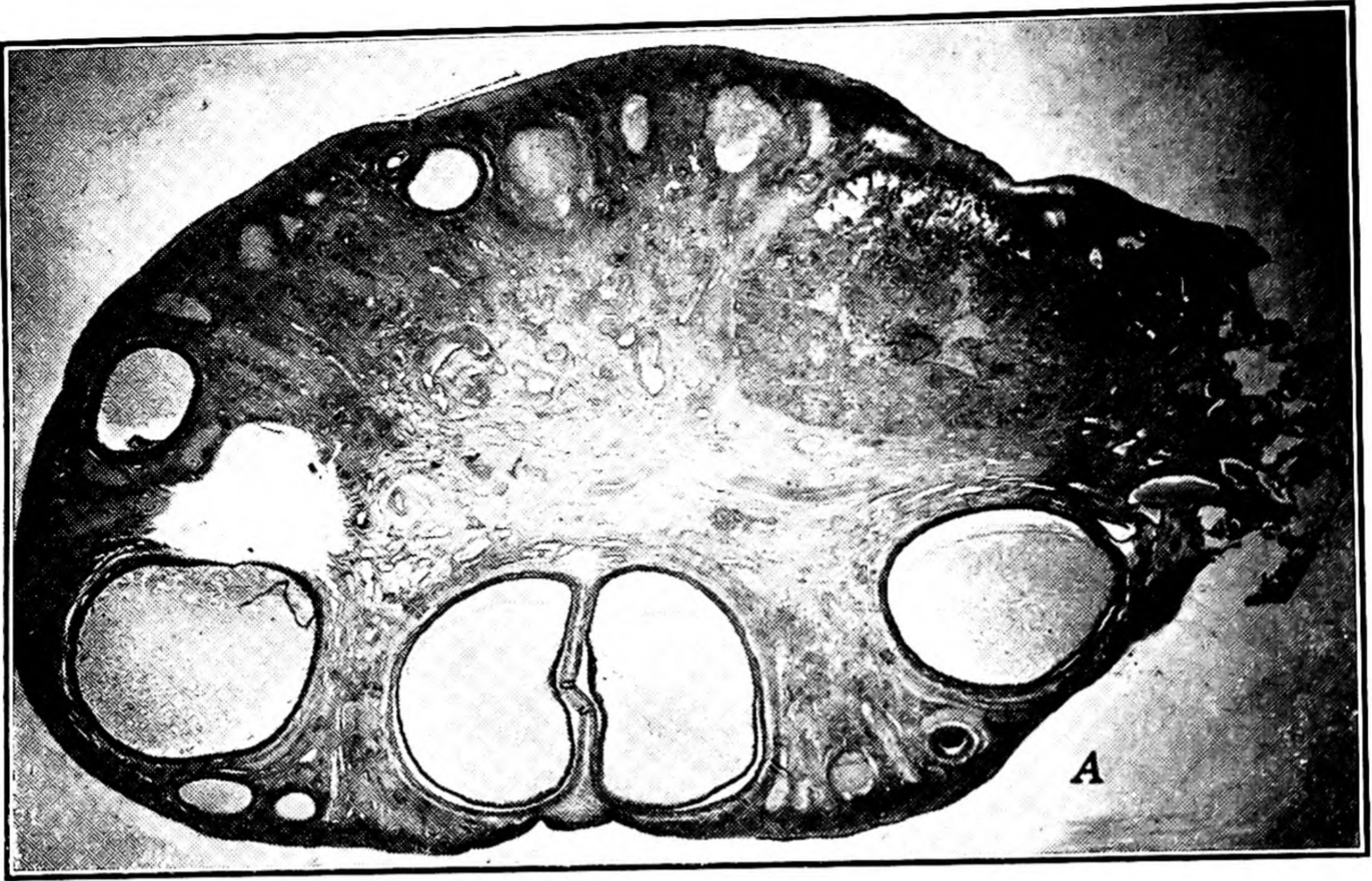


FIG. 15. Section through the ovary of the adult. (A) Normal functioning ovary of cow. (B) Cystic ovary of sow.

size they are about 20 to 22 inches from the vulvar orifice and in the cow, about 16 to 18 inches. In the cow they may be readily located by rectal palpation, but this operation is somewhat more difficult in the mare, especially in large mares.

The ovaries are much smaller than the testicles. In the mare they are about 3 by 1½ inches and somewhat bean shaped. In the cow they are about 1½ by 1 inch and rather oval in shape. In the sow they are proportionately much larger, and usually they have an irregular lobulated appearance.

Peritoneum covers the entire ovary except the attached border where the vessels and nerves enter. Germinal epithelium forms the surface of the ovary. In most animals the ovary is somewhat divided into a cortex, in which the follicles with the developing ova are located, and a medulla which is rich in blood vessels, lymphatics, and nerves. A network of connective tissue forms the stroma or supporting tissue of the ovary. The egg sacs or Graafian follicles are located between the meshes of the stroma. One Graafian follicle usually contains only one developing ovum. The follicles vary in size according to their stage of development; the more advanced project the surface of the ovary slightly. At maturity the follicle ruptures, thus allowing the egg and follicular fluid to escape. This is ovulation.

The Fallopian Tubes. These tubes lead from the ovaries to the horns of the uterus. They are about 10 to 12 inches long in the sow, cow, and mare. In the ewe they are slightly shorter. Their diameter is very small, especially at the uterine end. The ovarian end, the ampulla, is somewhat larger; at the ovarian extremity it becomes slightly funnel-shaped to fit around the ovary.

A serous coat covers the tube, fibrous tissue and some muscle furnish support, and a mucous coat lines the tube. The epithelium lining is of single-layered columnar ciliated cells. It is assumed that the cilia produce a current which forces the ova toward the uterus. Some force other than gravity must move the ova toward the uterus because the tubes are greatly coiled.

The Uterus. Implantation of the fertilized egg and development of the embryo occur in the uterus. The uterus is a hollow muscular organ which is capable of expanding greatly, as it does during pregnancy. The uterus consists of two horns, the body, and the neck or cervix. The horns are continuous with the ova

ducts but they are much larger. In most species the line of demarcation is quite sharp, but in others the one blends into the other gradually. The horns are about 10 inches long in the mare, about 15 inches in the cow, 6 inches in the ewe, and may be 4 or 5 feet in the sow.

The body of the uterus is about 8 inches long in the mare, $1\frac{1}{2}$ inches in the cow, 1 inch or less in the ewe, and 2 inches in the sow.

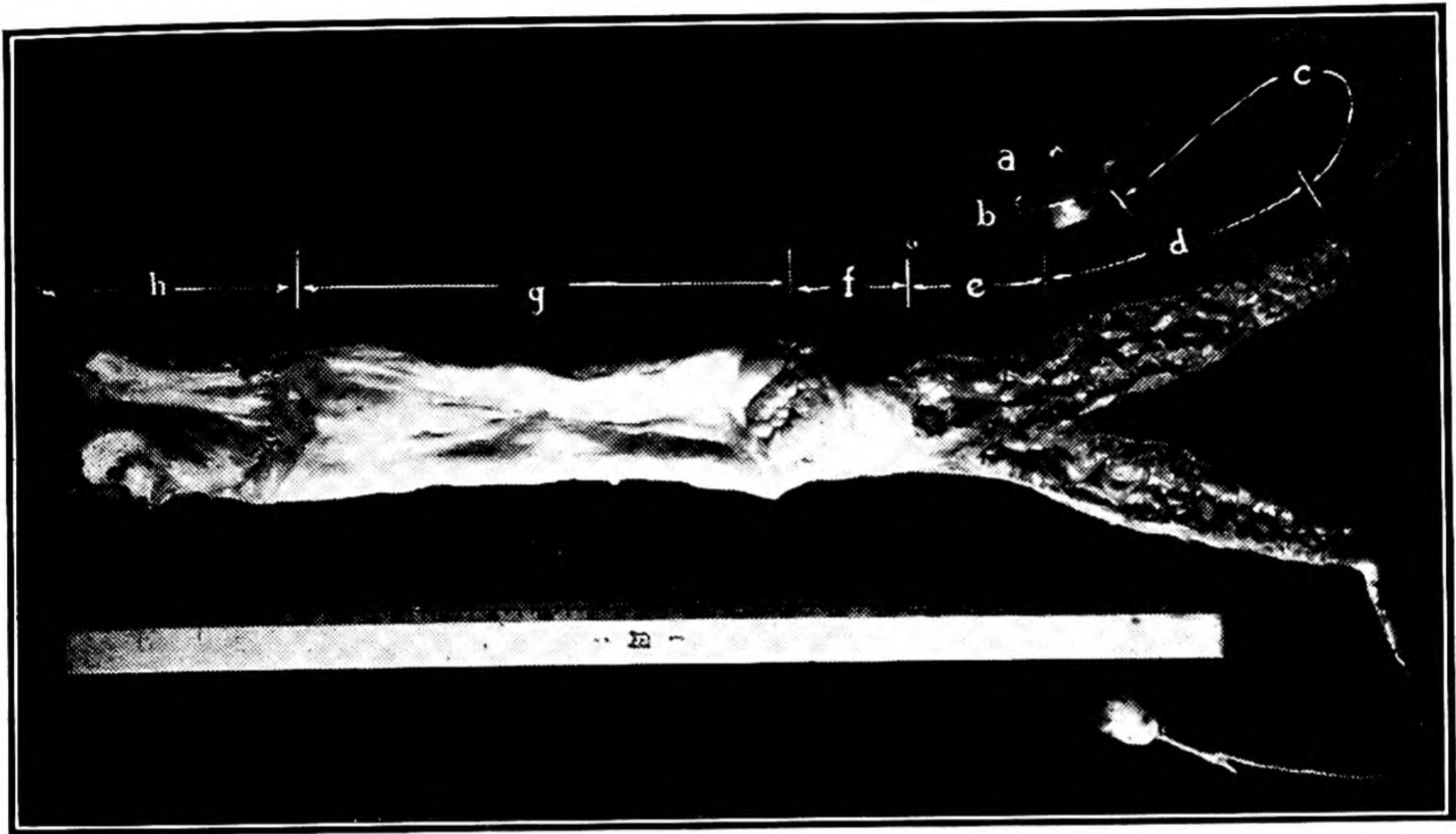


FIG. 16. Reproductive organs of the cow with the dorsal portion of the vulva, vagina, and uterus removed.

a, Ovary; *b*, a ripening follicle; *c*, ova duct; *d*, horn of uterus; *e*, body of uterus; *f*, cervix; *g*, vagina; *h*, vulva.

There are three layers in the uterine wall: serous, muscular, and mucous. The muscular layer is essentially two-layered, the external being rather thin and of longitudinal fibers, whereas the inner is thick and of circular fibers. Between the two is a vascular layer of connective tissue. The mucous membrane is covered by a single layer of high columnar cells and contains numerous uterine glands. In the cow and ewe the mucous membrane is marked by a number of prominences, the uterine cotyledons. The cotyledons serve as connections between the uterus and the foetal membranes. Each cotyledon has a deep face with a hilum at which the vessels enter.

The neck or cervix projects into the vagina. In the mare it is about 2 to 3 inches long and $1\frac{1}{2}$ inches in diameter, in the cow

it is about 4 inches long and 1 inch in diameter, in the ewe it is about 2 inches long and 1 inch in diameter, and in the sow it may be 6 inches long.

The circular muscular coat is very thick about the cervix and forms a strong sphincter. In the cow the lumen is spiral and usually closed tightly; in the ewe the lumen is closed by prominences and depressions of the mucous membrane.

The Vagina. The vagina is a passage extending horizontally from the cervix to the vulva. It is an organ of copulation. It, like the body of the uterus, has developed from the fusion of the embryonic Müllerian ducts. The vagina is separated from the uterus by the cervix and partially separated from the vulva by the hymen, a fold which narrows the entrance to the vagina.

The wall of the vagina is composed of two coats, the outer one being muscular and the inner, mucous. The muscular coat has a thin layer of longitudinal fibers and a relatively thick layer of circular fibers. There is also considerable intermuscular connective tissue in its walls. The mucous coat is covered with a stratified epithelium. The vagina like the uterus is highly elastic and is capable of great dilation which is necessary in giving birth to young. The vagina has no glands.

The Vulva. The vulva, also known as the urogenital sinus, is the terminal organ of both the urinary and the genital systems. It is a continuation of the vagina, and the urethra leads to its floor. The diameter of the vulva is considerably larger than that of the vagina. The walls of the vulva are well supplied with glands which are especially active during sexual excitement.

The clitoris lies partially imbedded in the posterior floor of the vulva. It is the homologue of the penis and excepting the urethra consists of the same parts.

SEX DIFFERENTIATION AND DEVELOPMENT

The Indifferent Stage. Early in the life of the individual it is impossible to distinguish its sex. At this time the gonads are in an indifferent state, giving no evidence as to whether they will develop into testes or ovaries; and the individual possesses two different duct systems. If the individual develops into a female one of the systems develops into the oviducts, uterus, and vagina, and the other system remains rudimentary. If the individual

becomes a male then the system which remains rudimentary in the female develops into the male duct system and the system that develops in the female remains rudimentary.

Development of the Gonads. The origin of the gonads is closely associated with the nephric system. In mammals and birds three distinct excretory organs occur. All three are paired organs and appear in succession, illustrating beautifully the law of recapitulation.

The *pronephros* appears in very young embryos but never becomes functional even in the higher fishes and amphibia. The *mesonephros* attains a high degree of development in the mammal but is replaced by the *metanephros* which becomes the permanent kidney.

Each gonad arises as a ridgelike thickening (gonadal ridge) on the mesonephros. The ridge thickens and becomes differentiated from the mesonephros. Some of the cells of the germinal epithelium become larger than the others; these large cells are called primordial germ cells. The exact site of origin of the primordial germ cells is not certain. One theory is that they arise by cell differentiation in the developing gonad, and another is that they arise in entoderm of the yolk sac and are carried to the germinal epithelium by the blood stream. Regardless of their previous history they are readily recognized in the germinal epithelium. If the gonad develops into a testis, the cells of the germinal epithelium grow into the underlying tissue and form cordlike masses which differentiate into the seminiferous tubules which produce sperm cells. If the gonad develops into an ovary the primordial germ cells grow into the underlying tissue and differentiate into the ovarian follicles which contain the ova. (See Chapter IV.)

Origin of the Sexual Duct Systems. While the embryo is in the indifferent stage two duct systems are equally well developed; they are the mesonephric and the Müllerian ducts. The mesonephric ducts are the excretory outlets for the excretions of the mesonephros. If the individual becomes a male they develop into the sperm ducts and the seminal vesicles. The epididymis arises from some of the mesonephric tubules which connect the mesonephros to the mesonephric duct. The prostate and Cowper's glands arise from the adjacent urethral epithelium.

If the individual becomes a female the Müllerian ducts develop into the oviducts, uterus, and vagina. The vagina and the body of the uterus are formed from a fusion of the two ducts.

The Müllerian ducts degenerate in the male, and the mesonephric degenerate in the female. Certain vestigial structures remain, however, in each case. The normal male has a structure called the appendix of the testis and a *uterus masculinus*, and the normal female has remnants of the mesonephric duct and tubules known as the epoöphoron and a faint counterpart of the *vas deferens* known as the canals of Gärtner. Under certain abnormal conditions these organs which should be vestigial develop partially; then the individual approaches the condition of the true hermaphrodite.

The External Genitalia. During the indifferent stage of the young embryo a central prominence (genital tubercle) appears; it is closely flanked by a pair of folds (genital folds), and farther to either side are rounded elevations called the genital swellings. If the individual develops into a male the genital tubercle elongates to develop into the penis, the genital folds form the prepuce, and the genital swellings enlarge to form the scrotal pouches. If the individual becomes a female the genital tubercle remains somewhat vestigial as the clitoris, the genital folds develop into the *labia minora*, and the genital swellings become the *labia majora*.

Sex Determination. Sex is inherited in essentially the same manner as other characters. (See Chapter X.) The genetics of the individual determines whether the gonads develop into testes or ovaries. It appears that hormones then become active (they may be at work earlier) and play a vital rôle in sex differentiation and development.

Gametogenesis and the Physical Basis of Heredity

Gametogenesis is the general process by which gametes are formed. An understanding and full appreciation of gametogenesis is fundamental to an understanding of heredity and the applications of modern genetic principles to animal breeding. The would-be student of animal breeding will do well not only to gain an understanding of how germ cells are produced but also to ponder its significance.

Primordial Germ Cells. Early in the life of the individual certain cells are set apart, the function of which is later to produce germ cells; they are known as primordial germ cells.

Opinions differ as to when the primordial germ cells are set aside. In the round worm, *Ascaris*, germinal and somatic tissues are specialized early in embryonic life; the differentiation can be distinguished when the embryo is in the two-cell stage, and at the sixteen-cell stage one of the cells is definitely limited to the formation of germ cells only; this cell is the first primordial germ cell. In the vertebrate embryo large pale cells which appear comparable to the primordial germ cells of the *Ascaris* can be recognized early. In some mammals, including man, they have been identified first in the caudal end of the body. From this distant point they migrate toward and into the sex gland. The nuclear behavior of these cells indicates that they are sex cells, but opinions differ as to their rôle and fate. One theory is that they are the progenitors of all future sex cells. Another theory agrees that these cells give rise to the early generations of sex cells but questions whether the final functional sex cells are the descendants of the early wandering primordial cells. In other words, the advocates of the second theory contend that it is unproved whether the eventual functional germ cells are the descendants of the primordial germ cells or of

the epithelium of the sex gland. A third view is that the above-described elements are but a transitory repetition of an ancestral type of parental germ cell and that they have no part in the actual formation of the egg and sperm of present-day mammals. The advocates of this theory contend that the germ cells originate by proliferation of the germinal epithelium.

For practical purposes it makes little difference which, if any, of the above theories is correct, for the end result is the same: germ cells are produced from specialized cells and they are produced in a systematic manner.

During the process of differentiation, both egg and sperm pass through a series of changes and stages which are essentially the same. The process by which sperm cells are formed is known as *spermatogenesis* and that by which eggs (ova) are formed is known as *oögenesis*. Each passes through three equivalent stages. The first is the stage of proliferation, which is marked by rapid proliferation of the primitive germ cells. The second is the growth period, which is the rapid enlargement or growth of the particular cell, or cells, that is, or are, about to give rise to a germ cell or cells. The third is the maturation stage, during which time important nuclear changes occur. The third stage is limited to the two final divisions and is followed by morphological changes in the male gamete.

At this point it is well to remind the reader that the chromosome number is constant for the cells of any given species of animal. In the round worm, *Ascaris*, the number is two. The chromosome numbers for some of our farm animals and man has been given as follows:

Cattle	60
Chicken (male)	36 and 74 (different workers)
(female)	35 and 73 (different workers)
Goat	60
Horse	60
Man	48
Sheep	54
Swine	38

It is, therefore, clear that maturation is of great importance. In vertebrates, reproduction is dependent on the union of male and female germ cells. Without some special provisions for the reduction of the chromosomes, fertilization would double the

chromosome number with each generation. Reduction of the chromosome number occurs during maturation. The significance of reduction on sex determination and inheritance will be brought out later in this book.

Spermatogenesis. Spermatozoa arise from the epithelial cells that line the tubules of the testis. A study of the cross section of the normal mature mammalian testis will usually reveal all

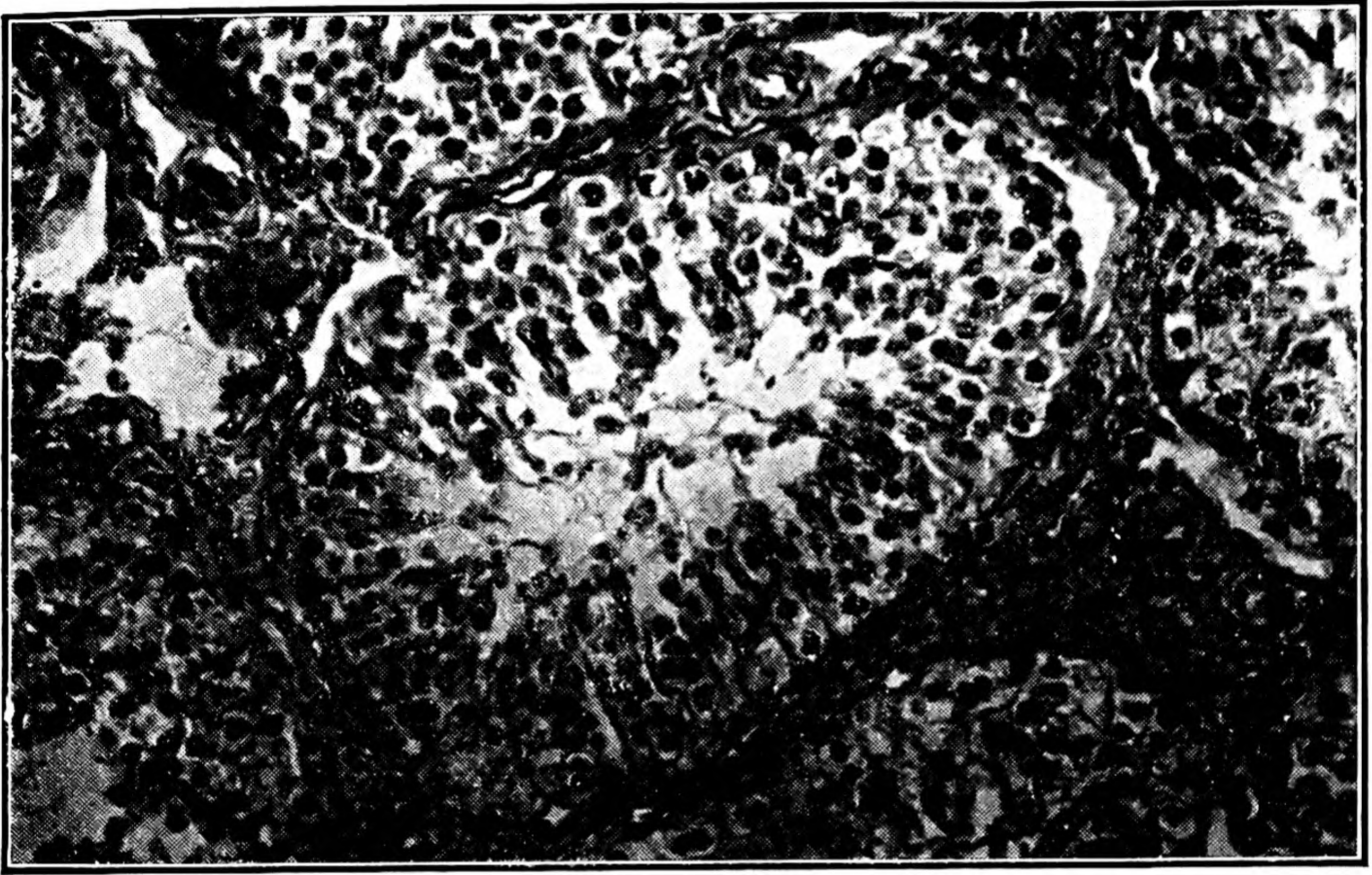


FIG. 17. Sections through the seminiferous tubules of the bull, catching the process of spermatogenesis as revealed by the camera.

stages of spermatogenesis. The cells within a tubule are of two distinct types. One type is very tall; they are the sustentacular cells known as *Sertoli cells*. Supposedly they lend support and serve as nurse cells to the ripening sperm cells. The second are the male germ cells. They are found in various stages of maturation and are arranged in a somewhat layered order. All the germ cells are the descendants of the primitive germ cells. The primitive germ cells after numerous divisions become *spermatogonia*. Until puberty spermatogonia and sustentacular cells are the only cells within the tubules. At the time of puberty activity within the testis increases markedly. By repeated mitotic divisions the number of spermatogonia increases. At the time of puberty some of the spermatogonia are regularly entering the growth period. At the end of this period they are known as

primary spermatocytes. So far as is known no qualitative change has occurred during the transition from a spermatogonium to a primary spermatocyte. Certainly there has been no change in chromosome number. There is an increase in the size of the cell, the nucleus is larger, and the amount of chromatin has increased markedly. Spermatogonia will be found close to the basement membrane; primary spermatocytes are found, for the most part, somewhat removed from the basement membrane.

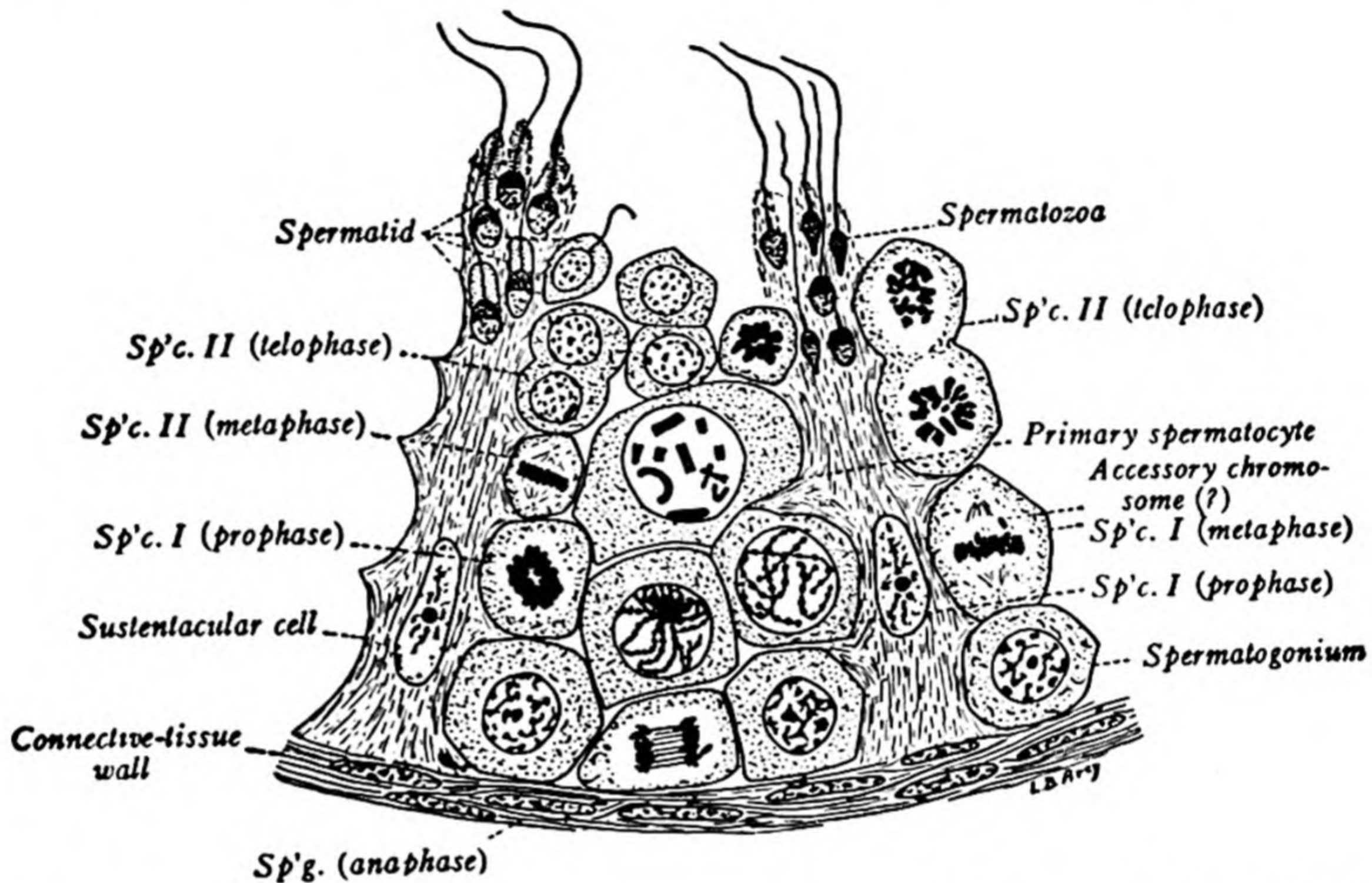


FIG. 18. A diagrammatic cross section of a seminiferous tubule illustrating spermatogenesis. (From Arey, *Developmental Anatomy*, W. B. Saunders Co.; reprinted by permission.)

It appears that they either work their way out or are pushed toward the lumen of the tubule as maturation advances.

The development of the primary spermatocyte is followed by two divisions which accomplish maturation. The primary spermatocyte divides into two *secondary spermatocytes*, each of which in turn divides into two spermatids. As the primary spermatocyte prepares for division, the chromatin becomes thread-like. At this time the chromatin also becomes gathered together as distinct chromosomes, the members of each pair coming to be arranged more or less side by side. A shortening of the chromosomes and at the same time a longitudinal split of each chromosome follows. Longitudinal splitting of the chromosomes often occurs previous to the shortening process and the conjugation of the pair members. The pair members usually come quite close together for a short time and give the appearance of having fused into a single strand. Shortly after this, two splits can

be recognized: one is the point of union of the two chromosomes, and the other is the split down each of the conjugated chromosomes. Each pair of chromosomes resembles four parallel strands and is known as a tetrad. At this time there usually is a twisting with results illustrated in Fig. 19. The twisting provides the mechanism for the exchange of chromatin between the pair members; this is the mechanism whereby crossing over takes place and has great significance in the transmission of hereditary material from generation to generation.

The next step is a separation of the tetrad into two diads. The diad members pull apart, one member going to each *secondary spermatocyte*. By this process two secondary spermatocytes have resulted from one primary spermatocyte.

The secondary spermatocyte then proceeds to produce two spermatids. In this division the bivalent members of the diad draw apart, and one member of each diad becomes included in each resulting spermatid.

A summary of this important series of events follows:

1. A spermatogonium grows to become a primary spermatocyte. No change in the chromosomes occurs at this time.

2. The primary spermatocyte goes through what is known as a reductional division, and two secondary spermatocytes result. Each secondary spermatocyte contains only one-half the number of chromosomes in the primary spermatocyte, and it is not any half but one member of each pair.

3. Previous to the above separation and reduction in chromosome number each chromosome starts to split lengthwise. The pair members, each of which is partially split, come together and form what is known as a tetrad. At this time there usually is a twisting of the tetrad which allows for the exchange of chromatin material between the members of the tetrad; this is **crossing over**.

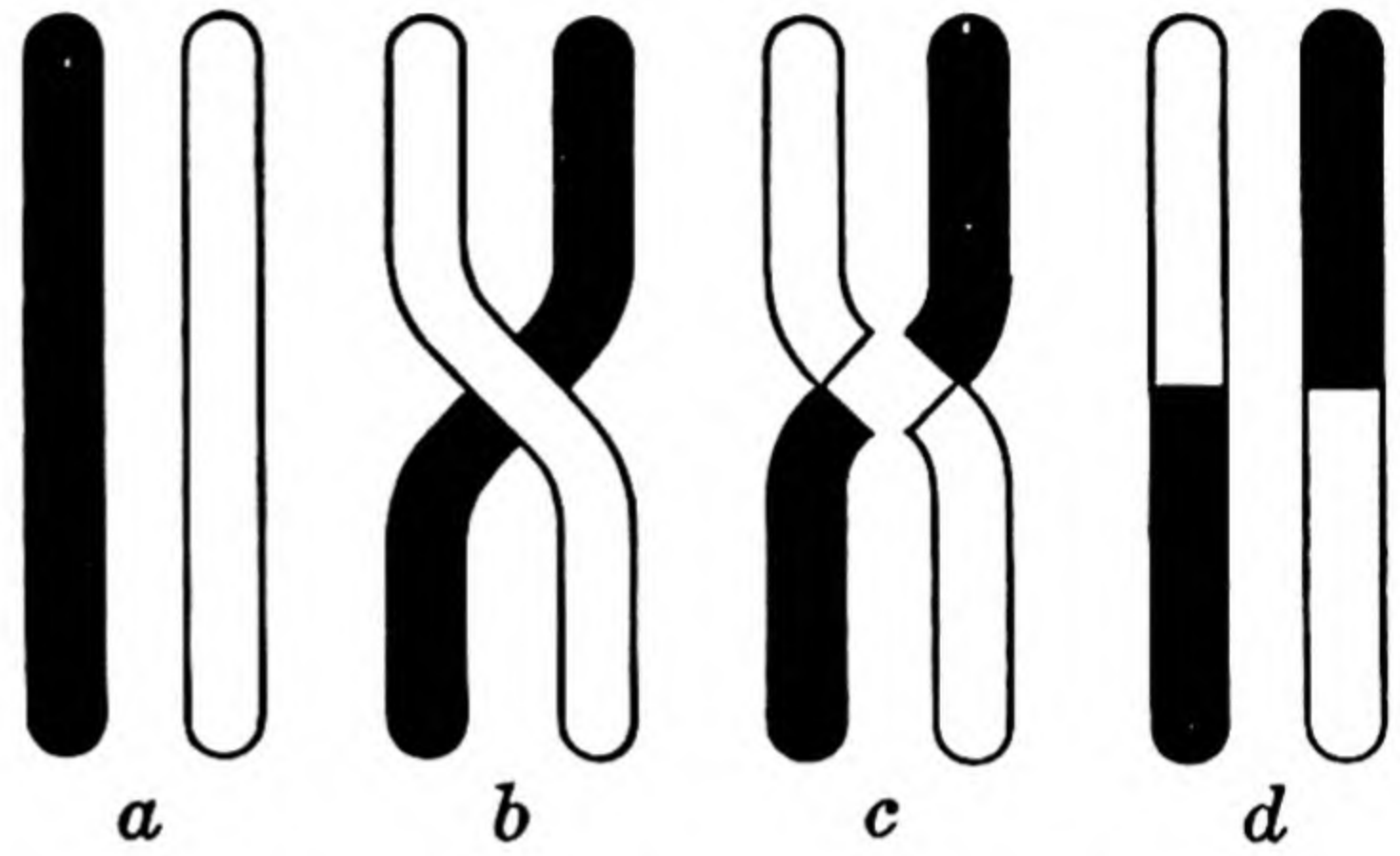


FIG. 19. Interchange of chromatin between homologous chromosomes. (After Muller, from Babcock and Clausen, *Genetics in Relation to Agriculture*, McGraw-Hill Book Co., Inc.; reprinted by permission.)

4. The secondary spermatocyte goes through another cell division, known as the *equational* division. In this division the members of each diad draw apart, and one member of each diad becomes included in the two resulting spermatids.

5. A primary spermatocyte, which has the diploid number of chromosomes, passes through a reductional division and produces two secondary spermatocytes, each of which contains the haploid number of chromosomes. Each secondary spermatocyte divides equationally and produces two spermatids each of which, therefore, possesses a haploid number of chromosomes.

The morphologies of the primary spermatocyte, secondary spermatocyte, and spermatid are very similar but the differences

in the amounts of chromatin are rather definite. The newly formed spermatid then enters a series of morphological changes by which it becomes converted into an elongated element with the chromatin material packed in the head region, behind which is a slender middle piece, and behind that a whiplike tail. Excess cytoplasm is discarded in the process. The greater portion of this change occurs while the ripening sperm cell is partially buried in a Sertoli cell. Because of this intimate relationship, it has been assumed that Sertoli cells impart sustenance to the metamorphosing sperm cells; this, however, is an assumption rather than a proved fact. When the morphological change is completed or nearly completed the newly formed

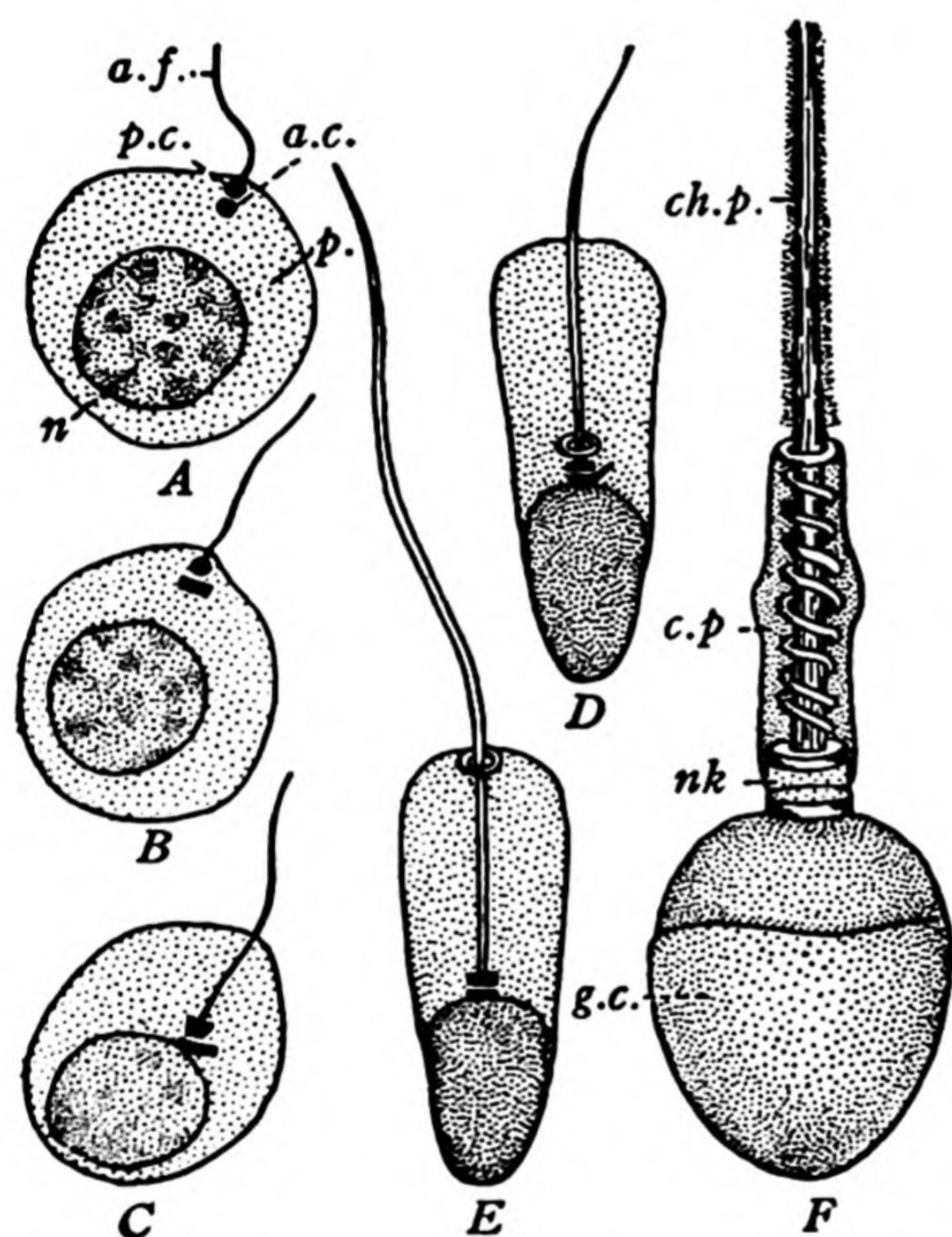


FIG. 20. Diagrammatic illustration of metamorphosis of a sperm cell. (After Meves, from Arey, *Developmental Anatomy*, W. B. Saunders Co.; reprinted by permission.)

a.c., Anterior centrosome; a.f., axial filament; c.p., connecting piece; ch.p., chief piece; g.c., cap; n., nucleus; nk., neck; p., cytoplasm; p.c., posterior centrosome.

sperm cell apparently is swept from the testis through the efferent ducts to the epididymis. The reason for this belief is that

sperm taken from the testis possess little if any motility and the secretory activity of the efferent ducts is high. Sperm cells apparently should go through a ripening process in the epididymis before they are in the optimum condition for fertilization. When males are used more frequently than is usual numerous sperm cells are ejaculated which have not completed their full metamorphosis.

Oögenesis. A cross section of the ovary will reveal ova in varying stages of maturation. Mature ova arise from a series of cell divisions closely paralleling those described for the production of spermatozoa. They originate from the germinal epithelium of the ovary. The primitive sexual cells are called *oögonia*; they are comparable to spermatogonia in the male. They, like the spermatogonia, contain the full (diploid) number of chromosomes and pass through an indefinite number of mitotic divisions. Oögonia like the spermatogonia go through a growth period by which they become *primary oöcytes*. The primary oöcyte divides to form the *secondary oöcyte*, and the secondary oöcyte divides to form the *ovum*. The mature ovum like the mature sperm cell contains only half the somatic number of chromosomes.

The divisions by which secondary oöcytes and ova are produced differ from those by which sperm cells mature in that there is an unequal division of the cytoplasm. Nearly all the cytoplasm goes to one daughter cell of the primary oöcyte. The one receiving little cytoplasm is known as a *polar body*. It may pass through a subsequent division but, whether it does or not, it and its descendent daughter cells are not functional. The secondary oöcyte carrying nearly all the cytoplasm of the primary oöcyte also passes through a division by which one daughter cell receives nearly all or all the cytoplasm; this cell is the mature ovum. The other daughter cell is called the *second polar body*, and like the first it also dies.

Another respect in which maturation of the ovum differs from that of the sperm cell is that the ovum matures within a follicle (Graafian follicle). Early in the life of the developing egg indifferent cells encase it. As the oögonium goes through its growth period these surrounding cells multiply many times and change their arrangement so that eventually a large follicle is developed within the cavity between the layers of cells. The fol-

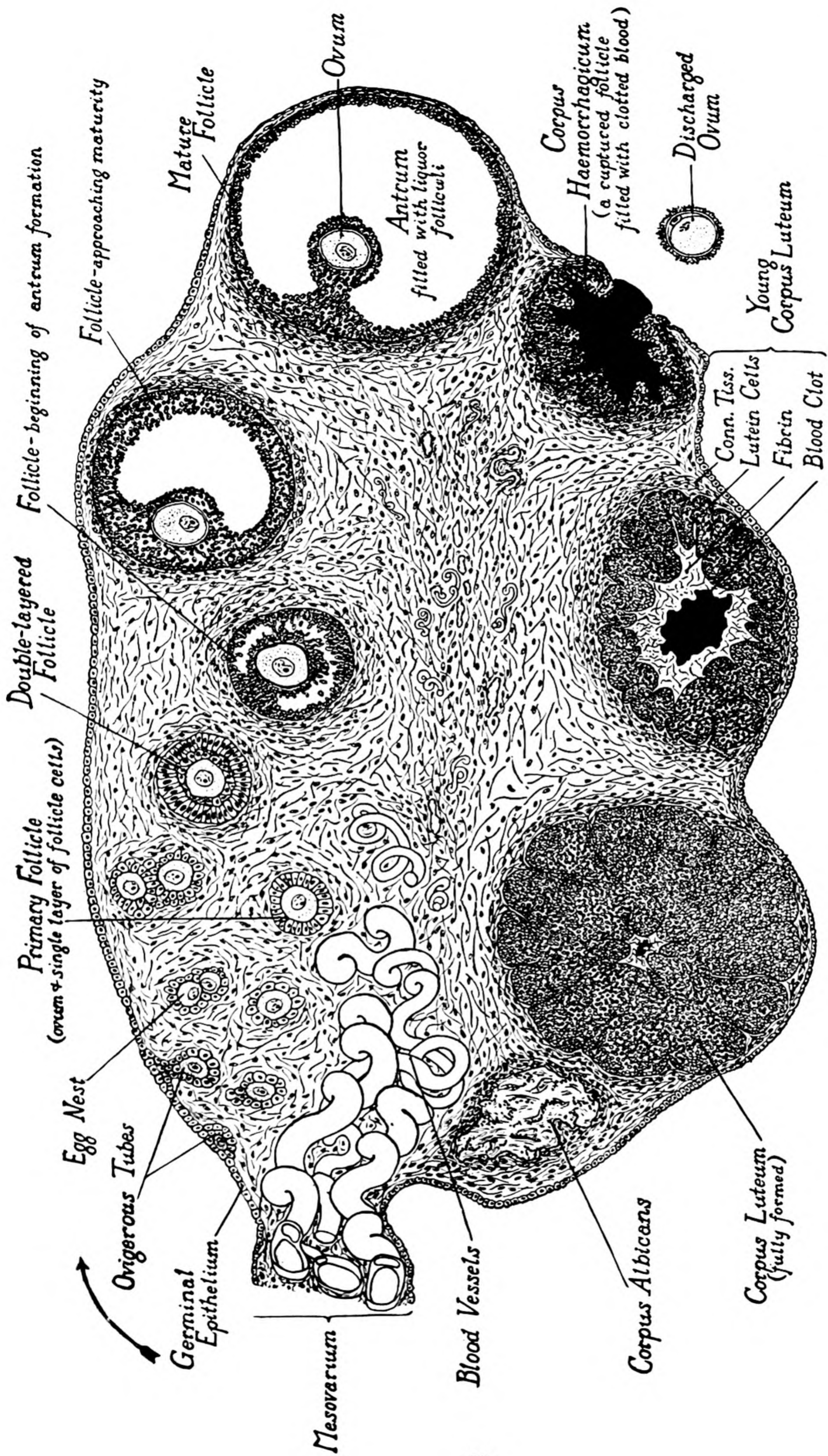


FIG. 21. Schematic diagram of mammalian ovary showing the sequence of events in the origin, growth, and rupture of the ovarian (Graafian) follicle and the formation and retrogression of the corpus luteum. (From Patten, *Embryology of the Pig*, copyright, The Blakiston Co., publishers; reprinted by permission.)

licle grows under the influence of a hormonal secretion from the anterior lobe of the pituitary. The layer surrounding the follicle

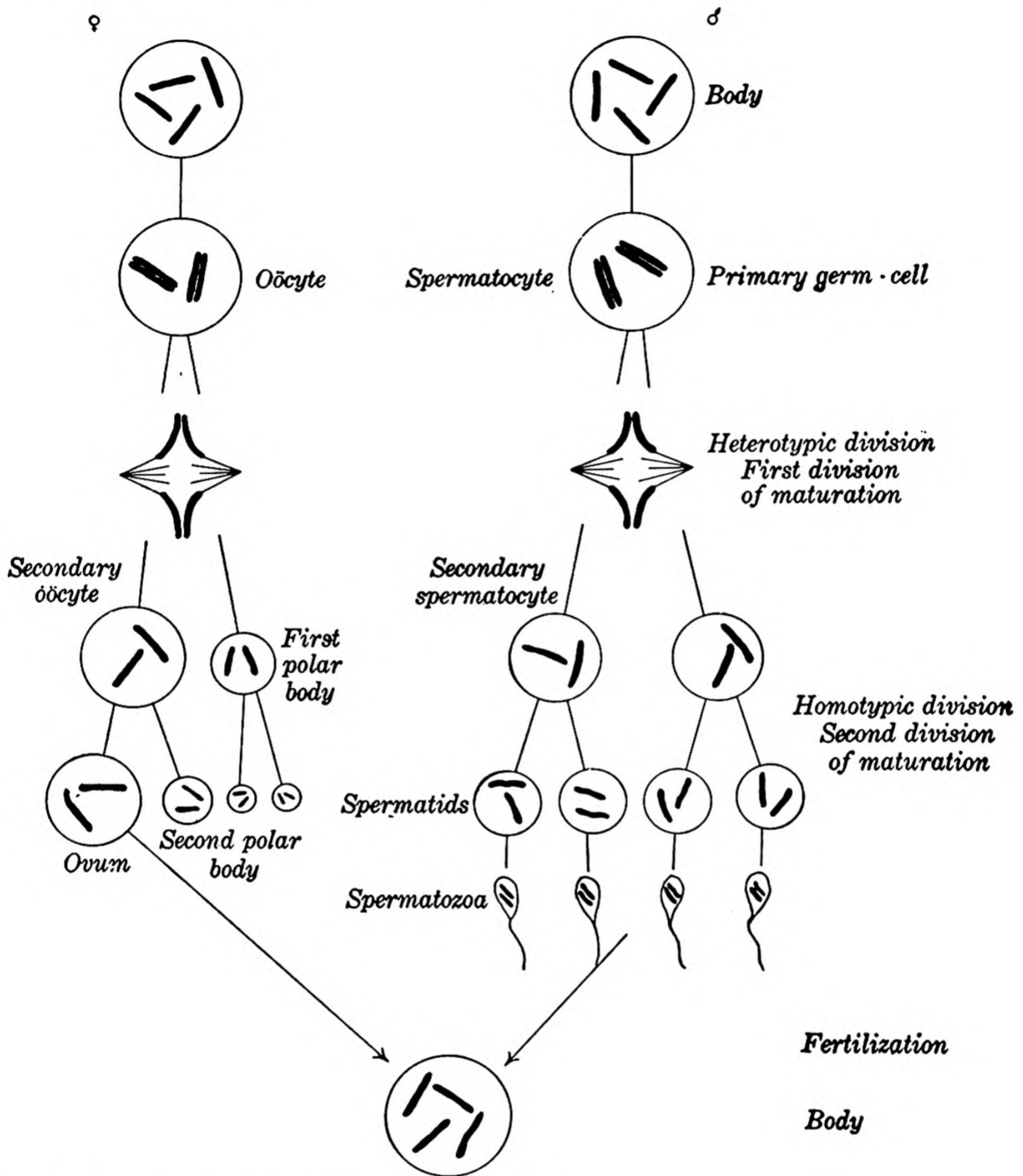


FIG. 22. Diagrammatic representation of the behavior of the chromosomes during the formation of the germ cells. (Modified from Sharp, *Introduction to Cytology*, McGraw-Hill Book Co.; reprinted by permission.)

is first a single layer of cells; later it develops into several layers. Soon a cavity is formed between these layers, and the cavity becomes filled with follicular fluid. This fluid contains what is commonly known as the female sex hormone, which stimulates

changes in the female reproductive tract and stimulates heat. As the follicle ripens it becomes very thin-walled and bulges the side of the ovary. Many follicles are ripening at the same time. In the mare and cow only one ovum is usually ovulated at a time. The other follicles, stimulated to a development which was not completed, then degenerate, and a fresh crop is stimulated for the following heat cycle. In the human being it is estimated that some 25,000 eggs and follicles are sacrificed for each menstrual cycle even though usually only one matures.

Ovulation. As the follicle develops it comes closer and closer to the side of the ovary. The wall thins out and the follicle comes to bulge the surface of the ovary. Considerable internal pressure is developed, for if the wall is pricked the fluid will spurt from the ovary. In normal development a thin clear area of the follicle protrudes like a nipple until it bursts and the fluid flows or in some instances spurts from the follicle. At this time the ripened egg is carried from the ovary, and ovulation is completed. The diameter of the sheep egg (outside the zona) is about 0.164 mm.; in the cow it is about 0.150 mm.

The ripe ovum is similar to the sperm cell in that it contains only half the somatic (haploid) number of chromosomes; it differs in that it is comparatively large, it is spherical in form, it contains much reserve food materials, and it is not capable of motion.

The rupture of the follicle is followed by hemorrhage; a blood clot then fills the old follicular cavity. After this process the cells lining the walls of the follicle (*stratum granulosum* cells) take on renewed activity. They secrete lutein cells which accumulate to become the *corpus luteum*. The corpus luteum (yellow body) then becomes an important organ of internal secretion. Its forced removal, during the early stages of pregnancy at least, is followed by abortion.

The Physical Basis of Heredity. The chromosomes provide the physical basis for heredity. The method by which chromosomes are passed from parent to offspring corresponds perfectly with the known facts regarding inheritance; the chromosomes by their behaviorism provide the perfect mechanism by which the details of segregation, independent assortment, linkage, and crossing over can be explained. The reduction of the chromosomes in gametogenesis and the subsequent recovery of the normal number

by fertilization are fundamental to a sound approach to an understanding of modern animal breeding. The student of animal breeding will, therefore, do well not only to gain an understanding of gametogenesis but also to reflect over and over again on its significance in the transmission of characters.

Chromosomes are not the factors of inheritance but they carry the factors. The factors are resident on the chromosomes and are symbolized as genes. A gene, however, as explained in greater detail in Chapter VIII, may have manifold effects: one gene may influence coat color, size, and viability, or some other combination of characters. The gene has not as yet been made visible to the eye, but through crossing over, translocations, and mutations the gene has been proved to be a definite unit of inheritance.

It is one of nature's many phenomena that the genes are carried by the chromosomes. There is also ample evidence that they are distributed lengthwise of the chromosome and that the distance between the different genes varies, yet each gene has its particular location, called locus, on a particular chromosome. For convenience in visualizing this situation we may picture each gene as a gem with its own particular position and setting in a broach set with many gems of different kinds and sizes arranged in a row. This arrangement, therefore, provides for the duplication of chromosomes and genes in the fertilized cell and all daughter cells but for only one chromosome and one gene of a given kind in each germ cell. (In rare instances duplicate genes have been identified in different loci.) The processes by which germ cells are produced, therefore, constitute the beginning of an understanding of animal breeding.

CHAPTER V

The Breeding Cycle and the Sex Hormones

The age of puberty marks the beginning of the young animal's ability to reproduce. At this time the gonads become functional; the testes commence producing sperm cells and the ovaries, ova. The onset of these phenomena is accompanied by profound changes in the growing animal which are the result of increased activity and readjustments of the endocrine system. New hormones are released within the system. At this time, the female is generally high strung or nervous, and the mammary glands increase noticeably in size.

The arrival of puberty in the male also is accompanied by temperamental changes; frequently the animals become nervous and pugnacious. As a rule marked physical changes occur; the forequarters, crest, and head undergo marked development, and in the horned breeds of sheep and cattle there is a thickening of the horns. These characteristics are known as secondary sex characters. Secondary sex characters manifest themselves in a variety of ways: males among the song-birds possess the beautiful voices, and in most birds males possess the brilliant plumage. Some of the latter may not be secondary sex characters but sex-linked characters.

In the selection of breeding stock and in the show ring great stress is frequently laid on the expression of secondary sex characters. However, the fundamental facts of both genetics and the physiology of reproduction, as well as some historic records of the breeds, do not justify this assumption, which has come to have so much importance in livestock judging. More emphasis is given to this point in Chapter XI, "Selection."

Age of Puberty. The age of reaching puberty is governed or influenced by the following factors: (1) genetic (species, breed, line, and individual); (2) sex; and (3) environment, especially

nutrition. As a general rule the representatives of the larger species and larger breeds within the species are slower in reaching puberty than the smaller ones. In general, males reach puberty later than females. Animals reared in a favorable environment and state of nutrition reach puberty earlier than those reared under less favorable conditions. Eckles (1927) has shown that well-fed heifers will, on the average, show oestrus three months earlier than those on a light ration.

There is considerable variability in age of reaching puberty but under farm conditions it is about as follows: the horse, 12 to 15 months; cattle, 8 to 12 months; swine 5 to 6 months; and sheep 5 to 7 months. Not all ewe lambs come in heat at this time, and those that do not generally do not mate until the following fall.

The Breeding Season. The breeding season is a certain season or seasons of the year in which females will mate. Their occurrence is influenced by heredity and environment, especially nutrition. In wild animals the breeding seasons are generally quite periodic but in most domestic animals the breeding season occurs at rather regular intervals throughout the year. This indicates that during the process of domestication and selective breeding genetic changes have been made in this regard. It is difficult, however, to be certain just how much of the change is due to a change in genetics and how much is due to changes in environment.

Cows, as a rule, will breed at regular intervals throughout the year although heat is usually more marked in late spring and early summer. Dairymen, as a rule, prefer to have cows freshen in the autumn but frequently have difficulty in keeping the herd on autumn freshening. Sows breed throughout the year. Mares are more likely to show decided signs of oestrus in the spring; some mares come in heat regularly throughout the year, whereas others will evince oestrus through the spring, summer, and autumn. Ewes of most breeds mate only in the autumn and early winter although in some breeds the mating season is extended over a much longer period. In the southwestern part of the United States many ewe flocks are moved in the spring or early summer from the hot lowlands to the mountains where it is cool and the sheep have fresh grass. Here the ewes breed and then drop lambs in the fall.

In some species, the males also go through definite breeding cycles. The period of rut is very prominent in the deer family; at that time the horns are well developed and the males are very pugnacious. During the non-breeding season the testicles go into a stage of quiescence and the males are as a rule quite docile.

Importers have long known that animals, when first introduced from foreign lands, often fail to breed but, after becoming acclimated, breed regularly. The same difficulty is often encountered when animals are moved from their home environment within the same country. The author has had considerable experience in moving breeding animals from one experiment station to another within the state and has learned not to expect the animals to perform as well in their new environment until they have been given considerable time in which to adjust themselves.

Considerable difficulty is frequently encountered in getting wild animals to breed in captivity. At first it was assumed that the failure was due to the changed surroundings and lack of natural exercise; but in most cases where a study was made of the animals' natural diet and a serious attempt was made to duplicate it the animals bred even better than their relatives in the wild state. Females that are milking heavily often fail to breed, and many females will not breed so long as they are nursing young.

It is well known that the anterior lobe of the hypophysis secretes hormones which stimulate sexual activity, but just why some animals respond more readily with the advent of warm weather and others with cool weather is not understood. Light is a factor in effecting sexual activity. In some birds gonads of both sexes are stimulated at any season of the year by increased exposure to light. The light apparently first stimulates increased activity of the hypophysis. This still, however, fails to explain why mares show increased sexual activity with the increased light and warmth of spring and ewes respond to either the shortened days or the cool weather of autumn or both.

The Breeding Cycle. Within the breeding season, heat appears in the normal female for the most part in quite regular cycles. Differences in length of cycle exist between individuals of a breed or species. Variations also occur in the length of cycle in the same individual, especially among females that are not

in the best of physical condition. Nevertheless a previous charting of the length of heat cycle for individuals is very useful in predicting the return of heat. The average length of cycle by species is about as follows: the mare, 21 days; cow, 19 to 20; ewe, 16 to 17; and sow, 20 days.

The cycle of heat (dioestrous cycle) is made up of four distinct phases which have been designated by Marshall as: (1) proestrus, (2) oestrus, (3) metoestrus, and (4) dioestrus.

Proestrus marks the animal's coming in heat. At this time changes are occurring in the reproductive organs. The vulva, vagina, and uterus become congested with blood, and the mucous lining becomes more active in secretion. Vaginal smears taken at this time usually possess a few large polymorphonuclear and mononuclear leucocytes, a few nucleated epithelial cells, and no cornified cells.

Oestrus, or heat, is the period when females will mate. Its duration varies with species and with individuals within a species. Here too, however, as in length of cycle there is some individual consistency; hence a previous charting of the duration of heat proves very useful for certain experimental work and for certain practices in breeding. As a rule, the heat period in the cow lasts 12 to 24 hours; in the ewe, 1 to 2 days; in the mare, 4 to 5 days; and in the sow, 2 to 3 days.

At this time the vulva becomes swollen and both vulva and vagina are congested with blood. Late in heat, vaginal smears possess many leucocytes and many acid-staining epithelial cells. Few or no cornified cells are present.

Metoestrus is the period when the organs return to a normal, non-congested condition. Vaginal smears at this time show many leucocytes and epithelial cells and a few cornified cells.

Dioestrus is the period of rest between heat periods. Vaginal smears at this time possess variable numbers of leucocytes and epithelial cells and few or no cornified cells.

THE SEX HORMONES

Hormones are produced by glands very similar to ordinary glands but differing in one respect at least: they are ductless. Their products are called internal secretions and are absorbed directly into the blood stream. They are then carried to vari-

ous regions of the body and may exert their influence on body parts far removed from their original source. The glands are called glands of internal secretion or *endocrine glands*.

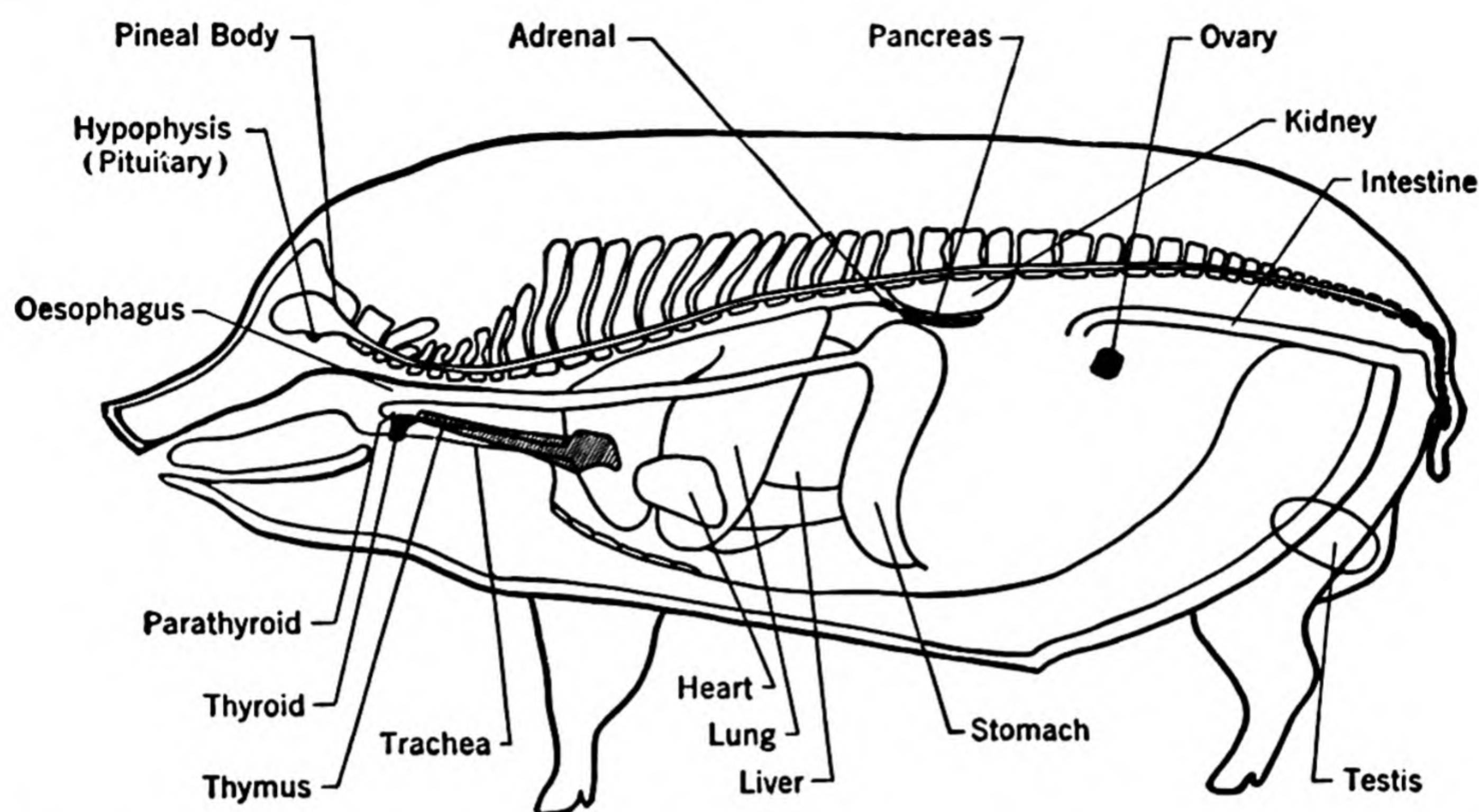


FIG. 23. Drawing of the pig indicating the locations of the principal glands of internal secretion.

The Hypophysis Cerebri. The hypophysis, frequently called the pituitary, is a small gland located at the base of the cerebrum in the cranial cavity. In this position it is remarkably well protected from physical injury.

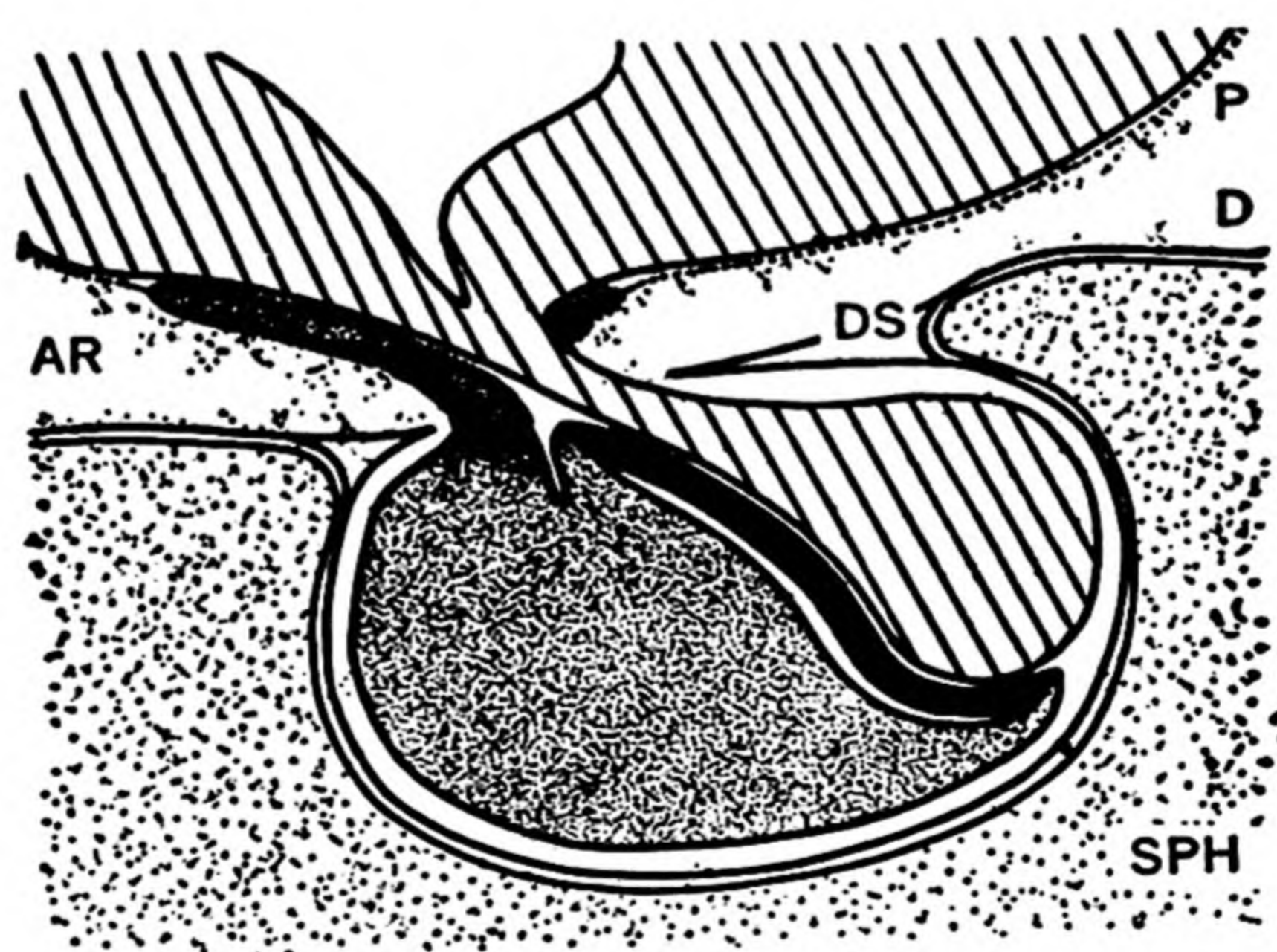


FIG. 24. Diagrammatic sagittal section of pituitary. Lined, brain floor and pars nervosa; fine stipple, pars distalis; coarse stipple, pars tuberalis; black, pars intermedia; SPH, sphenoid bone; P, pia mater; D, dura mater; DS, diaphragma sellae; AR, arachnoid spaces. (After Atwell in *New York Medical Journal*; reprinted by permission.)

This gland arises from two originally distinct primordia which become associated to form the hypophysis. One primordium arises from the primitive mouth and the other from the diencephalon. The first develops into what is recognized as the glandular portion, *pars buccalis* or *pars glandularis*; the latter develops into what is known as the posterior lobe, *pars neuralis*. Each of the two major portions is in turn divided histologically into subdivisions. An outline of component parts of the hypophysis follows:

1. *Pars buccalis* (glandular portion)
 - a. *Pars juxtaneuralis* (intermediate portion)
 - (1) *Pars tuberalis*
 - (2) *Pars infundibularis*
 - b. *Pars distalis* (anterior lobe)
2. *Pars neuralis* (posterior lobe)
 - a. *Eminentia sacularis*
 - b. *Infundibulum*
 - c. *Processus infundibuli*

The hypophysis cerebri is spoken of as the master gland of the endocrine system; it is essential to health and normal growth. A large number of hormones have been attributed to this small gland, and more are being attributed to it. The better-known hormones are identified and discussed briefly below.

Anterior Lobe. Tethelin, the growth hormone, is a product of the anterior lobe. Excessive secretion (hyperpituitarism) of this hormone produces the pathologic condition of gigantism, and deficient secretion (hypopituitarism) results in incomplete skeletal development, a condition known as dwarfism. Evans and Long (1921) produced gigantism in rats by repeated injections of the hormone; at the end of the treatment an experimental animal weighed 596 grams, and a healthy litter mate carried as a control weighed only 248 grams.

The anterior lobe produces a gonadotropic substance which is subdivided into the follicle-stimulating hormone (*FSH*) and the luteinizing hormone (*LH*). The chief function of *FSH* appears to be gametogenic. It regulates growth and rupture of the follicle in the female; in the male it appears necessary for conditioning of the seminiferous tubules. The result is that germ-

cell production in either male or female is apparently not possible without an adequate supply of *FSH*.

The *LH* stimulates the interstitial tissue and the seminiferous epithelium of the testis, and in the ovary it causes the transformation of the follicle into a corpus luteum. The interstitial cells of the testis in turn produce a hormone which stimulates growth of the accessory sex organs and secondary sex characters. The *LH* is, therefore, indirectly responsible for sexual maturity and the development of some secondary characteristics. In the female its main effects are to complement the *FSH* in causing ovulation, to cause formation of the corpus luteum from the granulosa cells of the follicle after ovulation, and to maintain the corpus luteum once it is formed.

It is clear that hormones play a vital part in milk secretion. A completely developed mammary gland may not lactate unless other factors are present to stimulate its initiation and maintenance of milk secretion. Peterson (1948) expresses belief that the following organs are all involved in milk secretion: hypophysis, thyroid, parathyroid, adrenals, and pancreas.

The thyrotropic hormone stimulates growth and function of the thyroid gland. Since thyroid activity directly affects metabolism, the anterior lobe exerts an indirect effect on metabolic rate.

The adrenal glands appear to be affected by two anterior lobe hormones: one that stimulates the adrenal cortex and another that stimulates the medulla.

All of the above directly or indirectly affect reproduction and lactation. Additional hormones ascribed to the anterior lobe are those stimulating function of the pancreas, the parathyroids, and the metabolism of nitrogen, carbohydrates, and fats.

Posterior Lobe. At least two products arise from this lobe; they are pitocin and pitressin. The former stimulates contractions of the uterus at the time of parturition. Pitressin assists in the control of blood pressure, stimulates peristalsis of the gastrointestinal tract, affects rate of respiration, and exerts both diuretic and antidiuretic effects.

The Thyroid. This is a much larger gland than the pituitary. It consists of two lateral lobes, and it lies below the larynx. Thyroxin is the active principle of the internal secretion. It speeds up metabolic processes of the body. An overactivity re-

sults in a high metabolic rate, a high pulse rate, a loss of weight, and muscular tremor. Low activity results in a low metabolic rate, a rapid increase in weight, and sluggish mental processes.

Thyroid activity affects testicular activity either directly or indirectly. It has been reported on rats that thyroid removal before sexual maturity retards the onset of spermatogenesis and that removal after maturity tends to decrease sperm production. Berliner and Warbritton (1937) have shown that a low level of thyroxin in rams is at least frequently associated with complete or partial sterility. Peterson and coworkers (1941) removed the thyroid of a young bull. The animal never attained normal size and exhibited no sexual interest, but sperm production appeared normal and by the aid of artificial insemination cows were settled with his sperm.

Adrenal Glands. The adrenal glands (suprarenal glands) are a pair of small glands situated slightly above the kidneys. They have two parts: a cortex and a medulla. These parts like the parts of the hypophysis arise from different sources. The medulla arises from the same region in the embryo that gives rise to the sympathetic nervous system. The cortex arises from the celomic epithelium very close to the urogenital fold.

Both the cortex and the medulla produce internal secretions. Adrenalin is a product of the medulla. When it is injected artificially the sympathetic nervous system is apparently stimulated because vasoconstriction, a rise in blood pressure, and acceleration of the heart follow the injection.

The cortex is necessary for life. When it is destroyed by disease, the patient develops a group of symptoms recognized as Addison's disease. These symptoms are progressive muscular weakness and emaciation; death follows.

The Testis. That removal of the testes in young males results in undeveloped secondary sex characters was known long before hormones were known as such.

The testicular hormone stimulates development and function of the accessory sex organs: epididymis, prostate, seminal vesicles, Cowper's gland, and penis. It also stimulates the development of what are known as secondary sex characters: the masculine head, heavy shoulders, coarse hair, and so on. A third effect is a stimulation of sexual drive.

During the full life of a normal male the testicular hormone appears to pass through four rather distinct periods. The first phase is prenatal. The assumption is, and there is some evidence to support it, that the testicular hormone stimulates the development of the male accessory organs. The fundamental factor determining whether the gonads develop into testes or ovaries is genetic. Differentiation of the gonad into testis or ovary is followed, normally, by the development of the accessory sexual organs appropriate to that sex. It appears that this development is stimulated by the testicular hormone in one case and the ovarian in the other.

The second period is the prepuberal one. During this period there is a finer and ultimate differentiation of parts. Gradual growth of the accessory organs occurs. At this time, the secretion, if any, apparently is at a low level. Studies by Hooker (1937) show that there is a gradual increase in hormone production throughout the first eighteen months of life in the bull. As a result of his studies, Hooker expresses belief that, in the bull at least, puberty is not a period of great and rapid change in hormone production by the testis, but rather that it is a period during which the tissues influenced by the hormone undergo changes even in the absence of a corresponding increased stimulation from the testis.

The third period is that in which the reproductive system is fully functional; this may be continuous as in most farm animals or it may be decidedly seasonal as in deer, ground-squirrels, and others. The difference between the two, continuous and seasonal breeders, appears to be that the gonadotropic activity of the hypophysis is continuous in one case and periodic in the other. It is assumed that activity of the hypophysis is stimulated by some environmental factor. In some birds increased light provides the stimulation. Increased light, however, has shown no effect on the ground-squirrel, but a decrease in light brings a response in the ferret and the sheep. It appears, therefore, that the different species respond to different stimuli. There are also some indications that animals in which breeding activity is continuous are subject to different levels of activity. Observations indicate that even in species where breeding activity is continuous different levels occur and that they occur by seasons and by cycles within the seasons.

The fourth period is that of senility. During this stage there is a gradual diminution of reproductive capacity. This phase is of much practical interest to livestock breeders because in the past many sires have reached the point of being proved sires and the age of senility at about the same time. Through a more complete understanding of the underlying factors, breeders may some day be able at least to delay the state of complete senility. Another approach which would accomplish the same practical end would be to speed up the processes by which sires are proved.

These four periods or stages in a male's reproductive state are very interesting. It appears that they are due primarily to varying degrees of stimulation from the anterior lobe of the hypophysis. It is possible that such stimulation is not the sole cause but that other hormones or varying physiological states may cause the animal body to be more receptive to hypophyseal stimulation at one period than at another.

The male hormone, testosterone, has been isolated from the bull testis. Other androgens also have been isolated or synthesized, but none has proved as potent as testosterone.

There is considerable evidence to support belief that the male hormone is produced by the interstitial cells of the testis. A cross section of a functional mammalian testis will reveal many seminiferous tubules, wherein sperm cells are produced and the interstitial tissue, as the name implies, is located between the many tubules.

Cryptorchid testes (undescended) of mammals become sterile because the abdominal temperature is higher than the scrotal. Increased temperature is destructive to the germinal epithelium of the testes. The germinal epithelium can be destroyed likewise through direct application of heat to the scrotum. Cryptorchid testes or heat-treated testes are sterile because the germinal tissue of the testis is destroyed. These testes, however, continue to secrete the testicular hormone, but there are indications that the hormone production is not so large as that from normal-functioning testes. It is, therefore, possible that the heat treatment reduces the potency of the interstitial cells; or it is possible, although it does not appear likely, that the germinal epithelium produces a hormone that either directly affects sexual activity or accelerates the interstitial androgens.

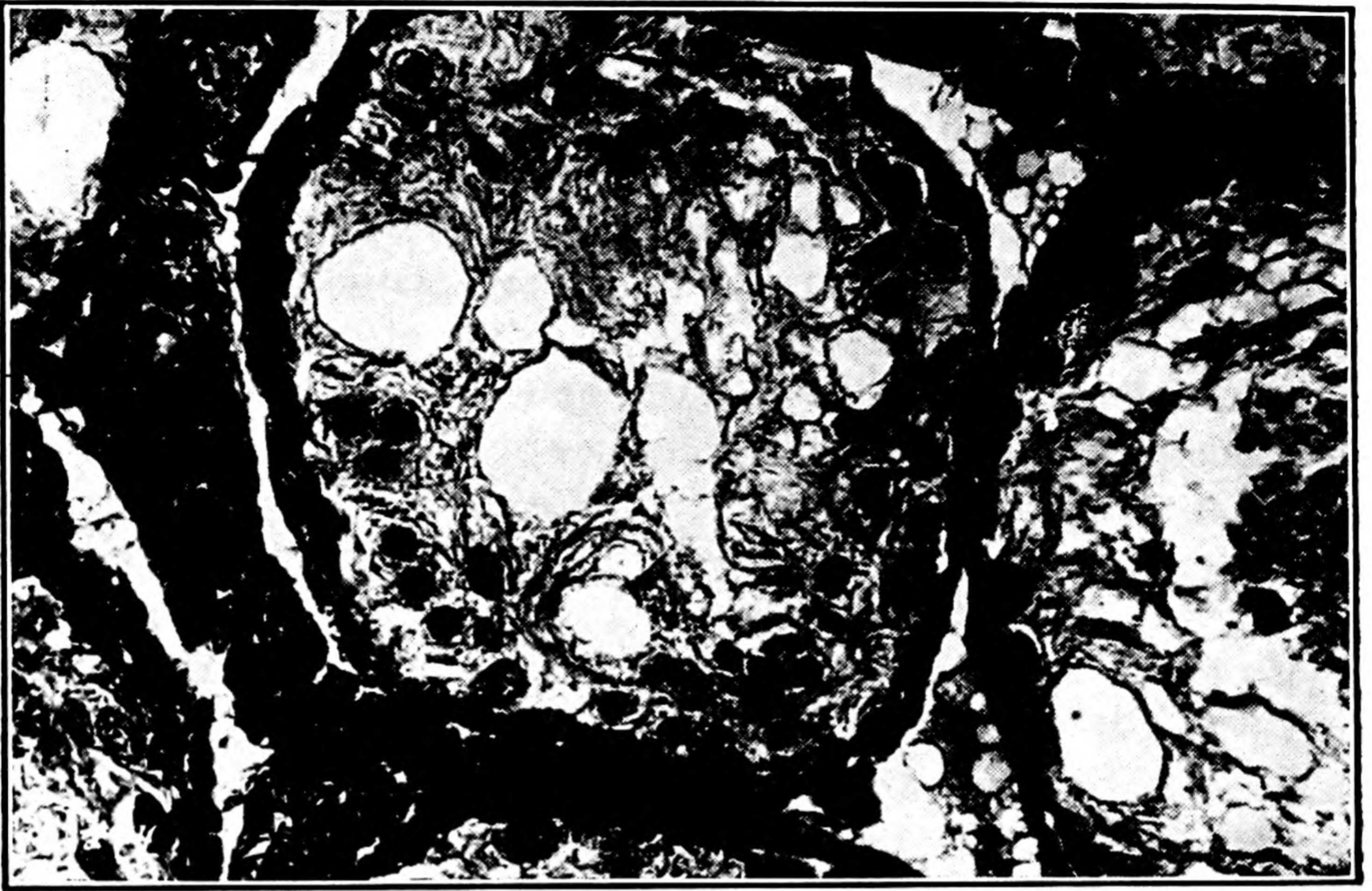


FIG. 25. Section through what should have been the seminiferous tubules of a cryptorchid rat. Note the absence of developing germ cells. Contrast with Fig. 17.

The Ovary. The ovaries serve essentially the same purpose in the female that the testes do in the male; they produce the germ cells and are the source of the hormone production that is essential to a functional reproductive tract.

Female germ cells in the mammal grow and ripen within a follicle. Within the follicle is follicular fluid, and this fluid contains the important female sex hormones such as estrogen, or estrogenic hormone. Originally it was thought there was only one female hormone, but it has been found that there are several, and the term estrogen, or estrogenic hormone, has been adopted to indicate any and all of the hormones of this group. Estrogen is also found within the corpus luteum.

Estrogen has diversified effects but the most significant are the stimulation of growth of the female reproductive tract and the mammary glands. The secondary sex characters in the female are dependent on this hormone as the secondary sex characters in the male are dependent on the testicular hormone. Ovariectomy is followed by atrophy of the accessory genital organs and retrogression of the secondary sex characters. Ovariectomy in imma-

ture animals is followed by lack of development of the accessory genital organs. It is also frequently followed by reduced physical activity and lack of sexual drive.

Estrogen serves as a regulator of the female reproductive tract and of the sexual cycle. In the adult it stimulates development of the uterine mucosa and thus aids the preparation of the uterus for reception of the fertilized egg. If the egg is not fertilized

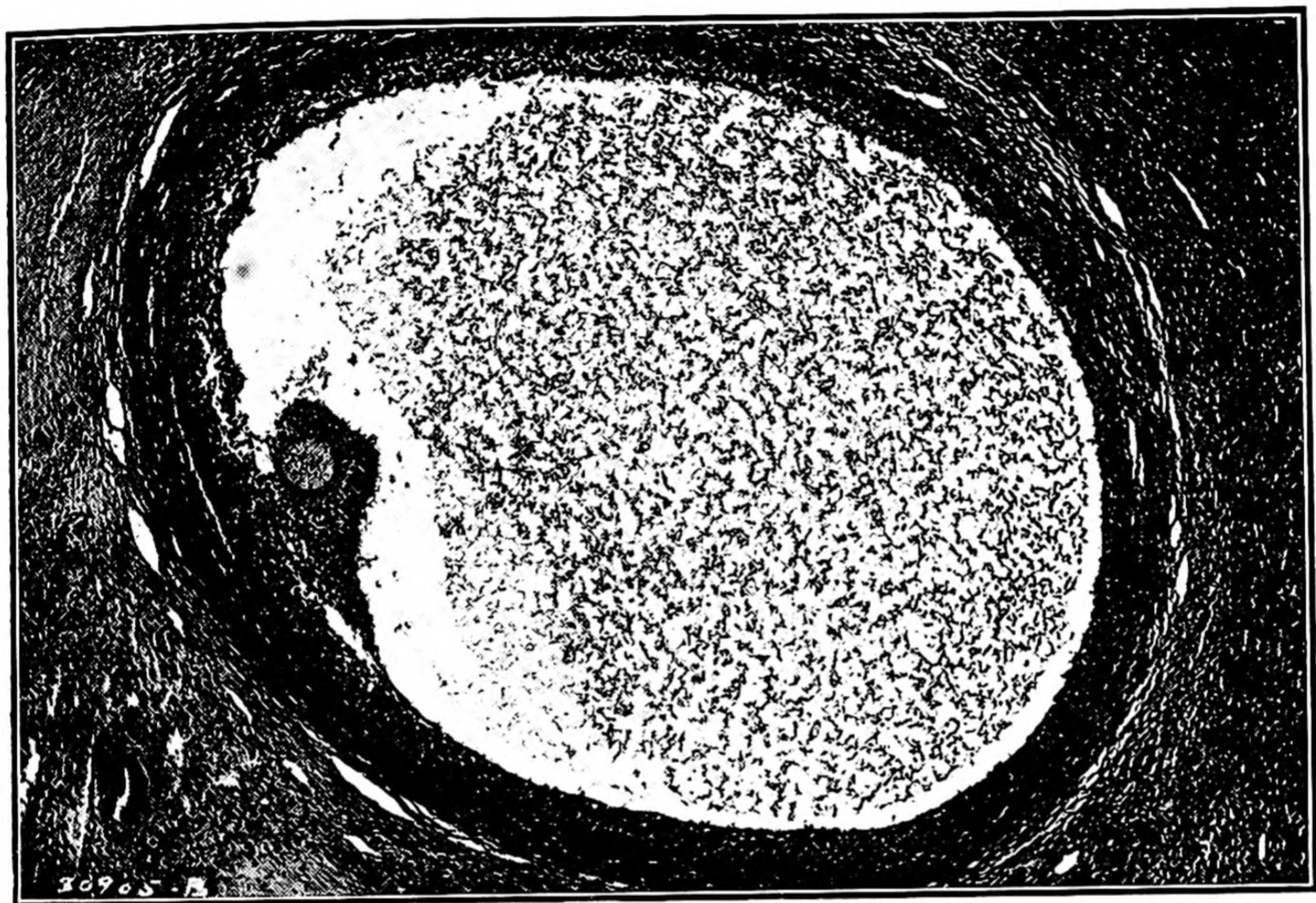


FIG. 26. Graafian follicle of the cow containing an ovum about ready to be ovulated.

or if the fertilized egg does not implant, the mucosa is shed, and a new mucosa development is stimulated by a new developing follicle or follicles. The development of the uterine mucosa can be stimulated experimentally by injections of estrogen. Estrogen also stimulates an increase in the rate and amplitude of uterine contractions. In addition it has a vasodilatory effect on capillaries of the endometrium.

Estrogen is also found in the corpus luteum and the placenta. Chemical compounds having estrogenic effects on the vagina have been isolated from the blood and urine of men and women (pregnant and non-pregnant), placenta, pussy willows, potatoes, various plants, and from the water of the Dead Sea. The amount present in male urine is rather constant but in female urine it

varies with the menstrual or oestral cycle. In non-pregnant women the maximum is reached about three to six days before menstruation. During pregnancy the amount increases after the eighth week, reaching a maximum about the time of parturition.

The Corpus Luteum. This organ, often called the yellow body, is a gland that develops within the ovary and is transient, its duration being largely dependent on the fate of the last ovum (or ova) released.

A relatively small amount of estrogen is found in the corpus luteum. Progesterone and relaxin are the chief hormones of this organ. Progesterone has the effect of continuing to stimulate the uterine development initiated by estrogen. It is necessary that this development of the uterus be continued; otherwise the uterine mucosa will not be in a satisfactory condition for the implantation of the developing ovum. Removal of the corpus luteum after implantation and through about one-third of pregnancy will usually be followed by abortion. Behavior and function of the corpus luteum varies according to species. In the horse and the human the corpus luteum has for the most part disappeared by the end of the first third of pregnancy. As the placenta develops it becomes an important source of progesterone, and apparently it gradually replaces this function of the corpus luteum.

Progesterone inhibits growth of the Graafian follicles, and, except on rare occasions, no further ovulations occur after implantation until after parturition. Apparently progesterone prevents the anterior lobe of the hypophysis from secreting the hormone necessary for follicular development.

Relaxin stimulates relaxation of the pelvic bones; this effect is especially marked in the guinea pig. Relaxin is produced in larger amounts shortly before parturition.

Interrelationship of Hormonal Action. As the hormones are becoming better understood, evidence of a strong interrelationship between the various hormones continues to accumulate. This interrelationship has been likened to that of an endless chain. There is little question that the hypophysis is the master gland, but it in turn is affected by overactivity or underactivity of other glands. All of them are affected by the general well-being of the animal.

At one time it was assumed that there was an antagonism between the then so-called male and female hormones. As more evidence has been gathered it has become clear that this assumption is not correct because both are normally found in both sexes. Under certain conditions it appears that the so-called male and female hormones have complementary effects.

CHAPTER VI

Fertilization and Prenatal Development

Fertilization is the union of the female and male germ cells, ovum and sperm. In mammals fertilization occurs in the uterine tube, usually the ovarian end. It is, therefore, necessary for the sperm to travel the full length of the uterus and most of the Fallopian tube before it reaches the egg.

Sperm Travel. The individual sperm cell appears much like a miniature tadpole and moves much like one.

At the time of copulation sperm cells are deposited in mass, and an active mass of sperm sets up a whirling motion of the semen that can be easily noticed when the semen is observed in a vial. The movement is quite rapid. Various conjectures have been advanced as to how sperm cells travel from the place of deposit to the upper end of the Fallopian tube. It may be that an active mass of sperm moves itself along much more rapidly than individual sperm.

In the mare semen is usually deposited in the uterus during coitus; hence it is not necessary for sperm to travel the full length of the uterus. In the dog, coitus is accompanied and followed by violent contractions of the musculature of the uterus and tubes that suck or pump the sperm toward the egg.

Parker (1931) has advanced the interesting theory that the cavity of the uterine tube is divided by its folds and muscles into a number of longitudinal compartments. The compartments next to the tubular walls have currents which move from the ovary, and the central compartments have currents which move toward the ovary. Eddies are thus formed which are assumed to work the sperm along the tube. The compartments are supposed to

be due to the muscular activities of the tube, and therefore the compartments are temporary.

Thus sperm are moved toward the ovary but of those that have been moved toward the ovary some would be moved back only to start the journey over again. If this theory is correct sperm are moved back and forth in the oviduct, but some are moved toward the ovary rather rapidly.

It is rather clear, however, that Parker's explanation is not the sole explanation of sperm travel because Phillips and Andrews (1937) found that, when a mixture of rat and ram sperm was injected in the vagina of the ewe, the ram sperm led in the race toward the ovary. It would appear that, if Parker's theory of sperm travel is correct, there should be a great variability in the length of time required for the ovum to traverse the oviduct but that does not appear to be the case.

Although considerable research has been conducted on methods of sperm travel, it is still not clear how sperm move or are moved from the cervix to the upper end of the oviduct. Research workers also differ markedly in their reports regarding the time required for sperm to travel from the cervix to the upper end of the oviduct. It is rather generally accepted that sperm travel is very rapid in the dog, but reports on the time necessary for sperm to travel in sheep and cows from the cervix to the end of the oviduct have varied from 7 hours to 3 minutes. The length of the uterus and oviduct constitutes a long journey for so minute an organism as the sperm cell and, since life is filled with many variations, it would be odd if there was not considerable variability in the time required for this journey. Both the method and the rate of sperm travel do have considerable bearing on fertility; therefore it is important that more research be conducted on both phases of travel. More information is needed regarding the factors affecting travel and the variations that are to be expected under normal conditions.

Semen. Semen is a rather milklike viscose fluid made up of secretions from the testes, epididymides, *vasa deferentia*, seminal vesicles, the prostate gland, and Cowper's glands. The amount of ejaculate varies with species of animals and with individuals within the species. Quantitative data on sperm numbers are presented in Table V.

TABLE V. QUANTITATIVE DATA ON SEMEN FROM SEVERAL SPECIES

(After Lambert and McKenzie, *U.S.D.A. Cir. 567*)

Animal	Volume per Ejaculate, Cubic Centi- meters	Sperm per Cubic Milli- meter	Total Sperm per Ejaculate	pH
Stallion	75-150	60,000	6,500,000,000	7.0-7.8
Bull	3-4	800,000	2,800,000,000	6.5-7.5
Ram	0.8	1,000,000	800,000,000	6.2-6.8
Boar	200.0	100,000	20,000,000,000	6.8-7.2
Dog	7.0
Fox	1.5		6.2-6.4
Buck (rabbit)	0.7	700,000	500,000	6.8-7.5
Turkey, tom	0.3
Cock	0.6		7.3-7.8

Marshall (1922) reports that human semen consists of about 90 per cent water and 10 per cent solids. Data on the analyses of semen from man, the horse, and the dog are presented in Table VI.

TABLE VI. SEMEN ANALYSES

(After Marshall, *The Physiology of Reproduction*)

	Horse	Dog	Man
Water	95.71	97.56	90.32
Total solids	4.30	2.45	9.68
Ash	0.92	0.69	0.90
Organic matter	3.38	1.76	8.78
All protein matter	2.24	1.26	2.85
Albumens, globulens, and nucleo-proteins	1.14	0.89 }	2.58
Mucin	0.56	0.06 }	
Albumoses	0.54	0.31	0.41
Lipoids	0.17	0.18	0.21
Cholesterin	0.004	0.0008	
Various organic substances	1.09	0.31	5.72

Viability of Germ Cells. Opinions differ as to how long germ cells remain alive within the female genital tract. Not many exact studies have been conducted on this point but all those that have been indicate that neither sperm nor ova remain alive for long. It is also quite clear that sperm cells lose their powers

of fertilization before they lose motility; in other words motility is no guarantee of fertility.

There are specie differences in regard to viability of germ cells. Egg cells are shorter lived than sperm cells. The life of the sheep ovum is probably less than 24 hours. In many mammals it probably is much shorter. The vast majority of sheep sperm cells are dead 24 hours after coitus; but fertilization in sheep has been known to occur 52 hours after coitus. This evidence was gathered by deduction: a ewe was bred previous to heat (ovulation occurs late in heat in the ewe); she was destroyed and the fertilized egg was recovered; the time of ovulation was calculated by comparing this egg's stage of development with that of other eggs of known age. Day (1942) has shown that horse sperm will remain fertile six days in the mare's reproductive tract.

In order that fertilization may follow coitus in cattle it is necessary for the sperm to live 24 hours or more, because ovulation does not usually occur in cattle until about 24 hours after heat has passed.

Fertilization has been reported to occur as late as 32 days after insemination in the hen and 10 days in the duck. The testes of the bird are, however, located within the body cavity; thus their sperm cells are probably better adapted to resist the higher abdominal temperatures, which are known to shorten the lives of most mammalian sperm cells.

Fertilization. In certain invertebrates the egg apparently produces a substance that at least promotes its union with the sperm. No similar substance is produced by the mammalian egg. There have been numerous conjectures regarding attraction between the two, powers of selectivity in the egg, and so on. It appears, however, that the union of the egg and the sperm is largely a matter of chance which sperm swimming along finds the egg in its path. On numerous occasions the author has placed a fresh unfertilized egg in saline solution under the microscope and then added fresh active sperm to one side of the dish. The sperms' course of travel was then observed. In not a single instance was a sperm observed to deviate from its path toward the unfertilized egg; sperm passed close by the egg but those that found the egg in their path made contact by burying themselves in the egg.

The zona of the fresh ovum is rather gelatinous. Only the head of the sperm penetrates the egg proper; the tail is left in

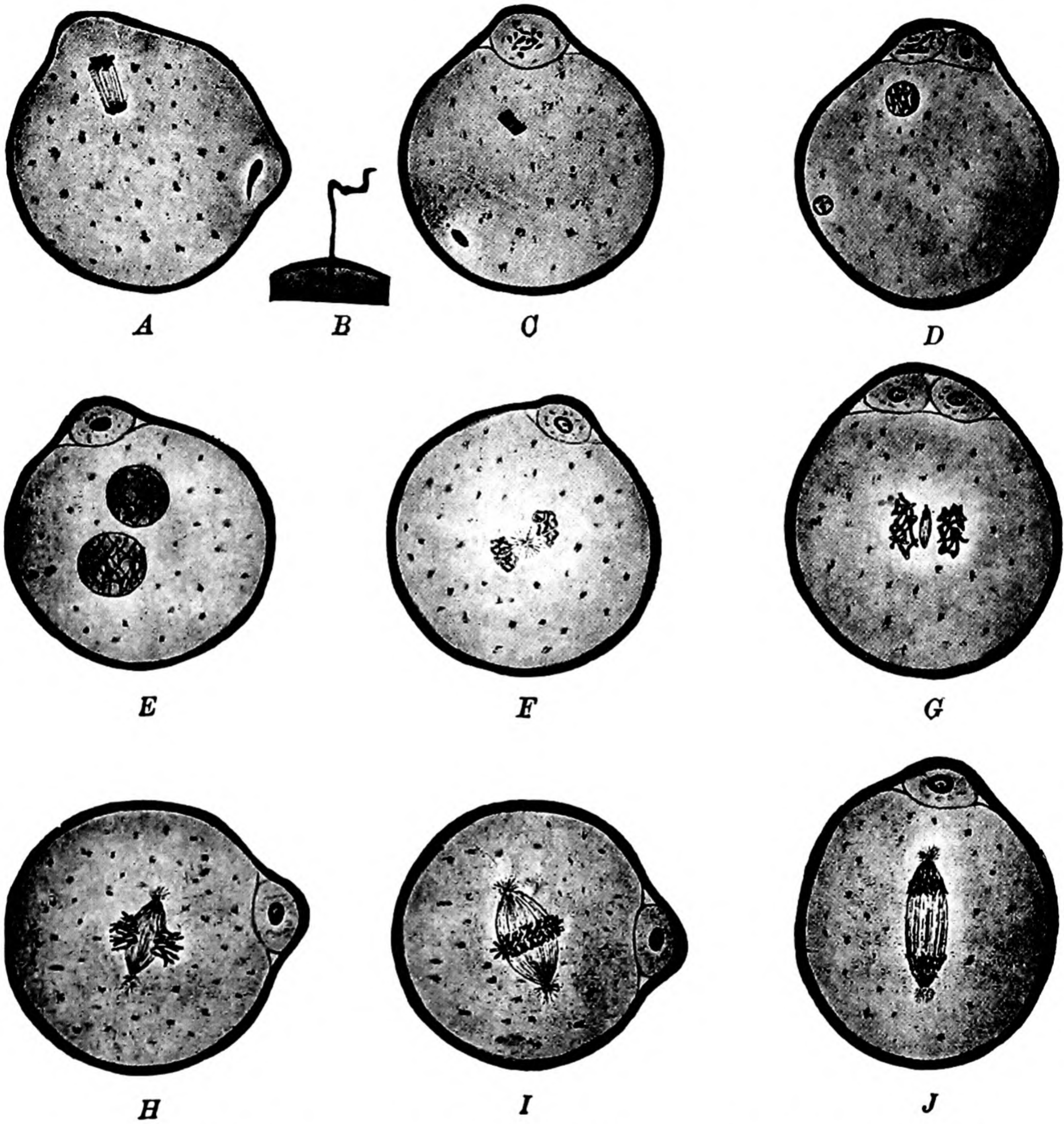


FIG. 27. Maturation and fertilization of the ovum in the mouse. (After Sobotta, from Bremer, *Textbook of Histology*, The Blakiston Co., publishers; reprinted by permission.)

A-C, Entrance of the sperm cell and formation of the second polar body; D-E, development of the pronuclei; F-J, successive stages in the first division of the fertilized egg.

the zona. Almost simultaneously with fertilization a fertilization membrane is thrown up around the egg, inside the zona; this membrane prevents a second sperm from fertilizing the egg.

Several sperm usually penetrate the zona but only one penetrates the egg proper.

The chromatin material appears to be packed almost solid in the sperm head. Once the sperm head is within the ovum it expands; the chromatin material reforms into chromosomes (the haploid number). It is now the male pronucleus. Frequently the second maturation division of the egg is not completed before the egg is released from the ovary; it may even be delayed until the sperm has penetrated the egg. The second maturation division always is completed, however, by the time the male pronucleus is formed. The reduced nucleus of the egg is the female pronucleus.

The two pronuclei approach each other and fusion follows; thus the normal number of chromosomes is restored to the egg, one member of each pair being supplied by the sperm and the other by the egg.

After formation of the pronuclei and before their fusion a mitotic spindle is formed from the centrosomal apparatus supplied by the sperm. The fertilized egg almost immediately goes into its first mitotic division.

Passage of Ovum down Oviduct. Whether the egg is fertilized or not, it slowly passes down the oviduct to the horn or the body of the uterus. The ovum itself has no powers of motility, and the greatly coiled condition of the oviducts precludes the possibility of gravity causing ova migration. During oestrus the oviducts of the sow exhibit a gradual increase in rate of muscular activity. This increase appears to be correlated with transport of the ovum, but it is uncertain what force moves the egg toward the uterus.

It is interesting and perhaps of some significance that about the same length of time, 3 to 4 days, is required in the ewe, the sow, and the cow for passage of the egg down the oviduct.

PRENATAL DEVELOPMENT

The new individual starts its life from the moment of fertilization rather than at birth, which is usually considered the beginning. A significant point is that at the time of fertilization the two parents have contributed all that they are capable of giving to the new individual's inheritance.

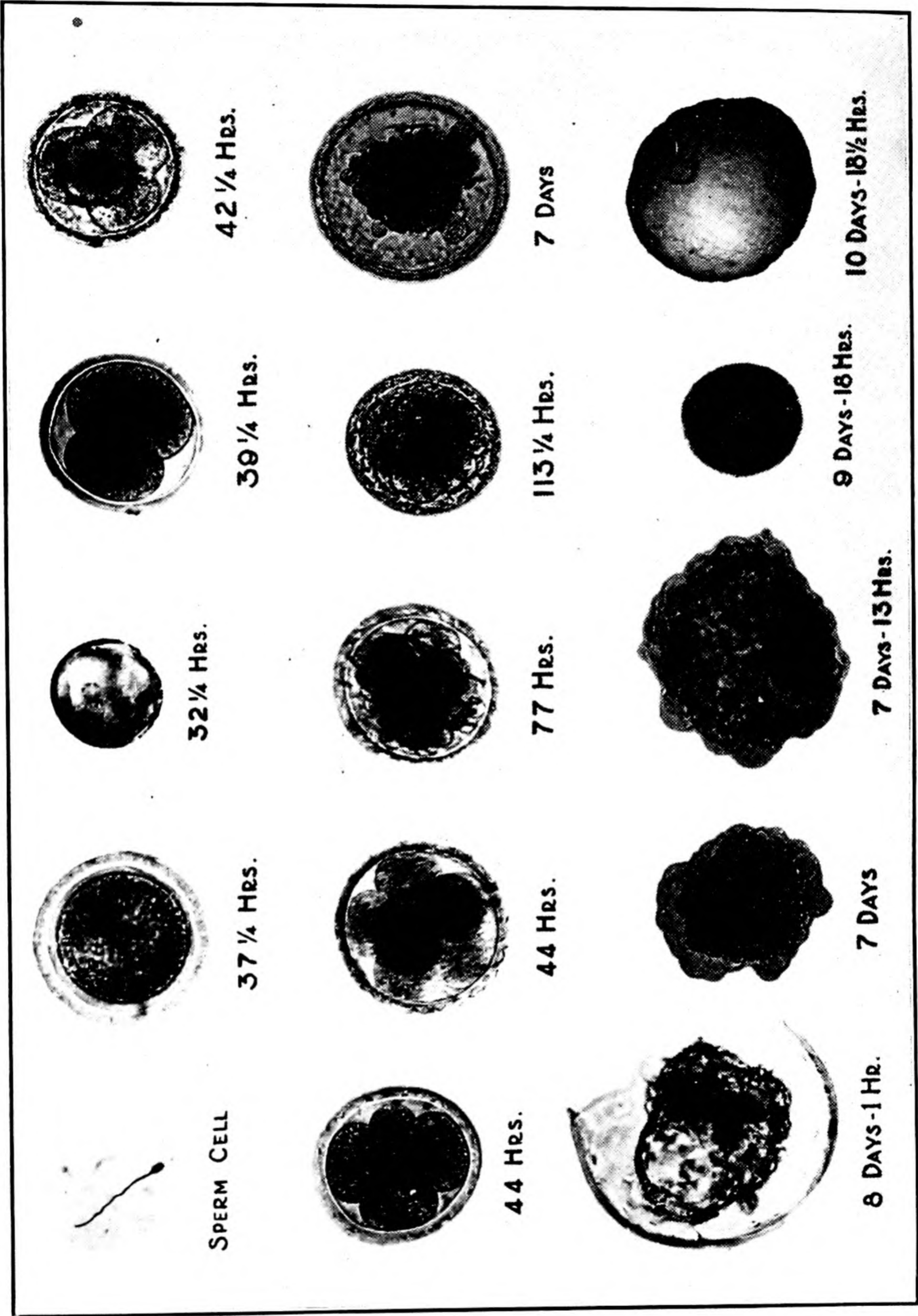


Fig. 28(a). The period of the ovum in the sheep. The 32 1/4-hour specimen is a sectioned egg; the two pronuclei can be seen. The 9-day 18-hour specimen fixed before being photographed appears smaller.

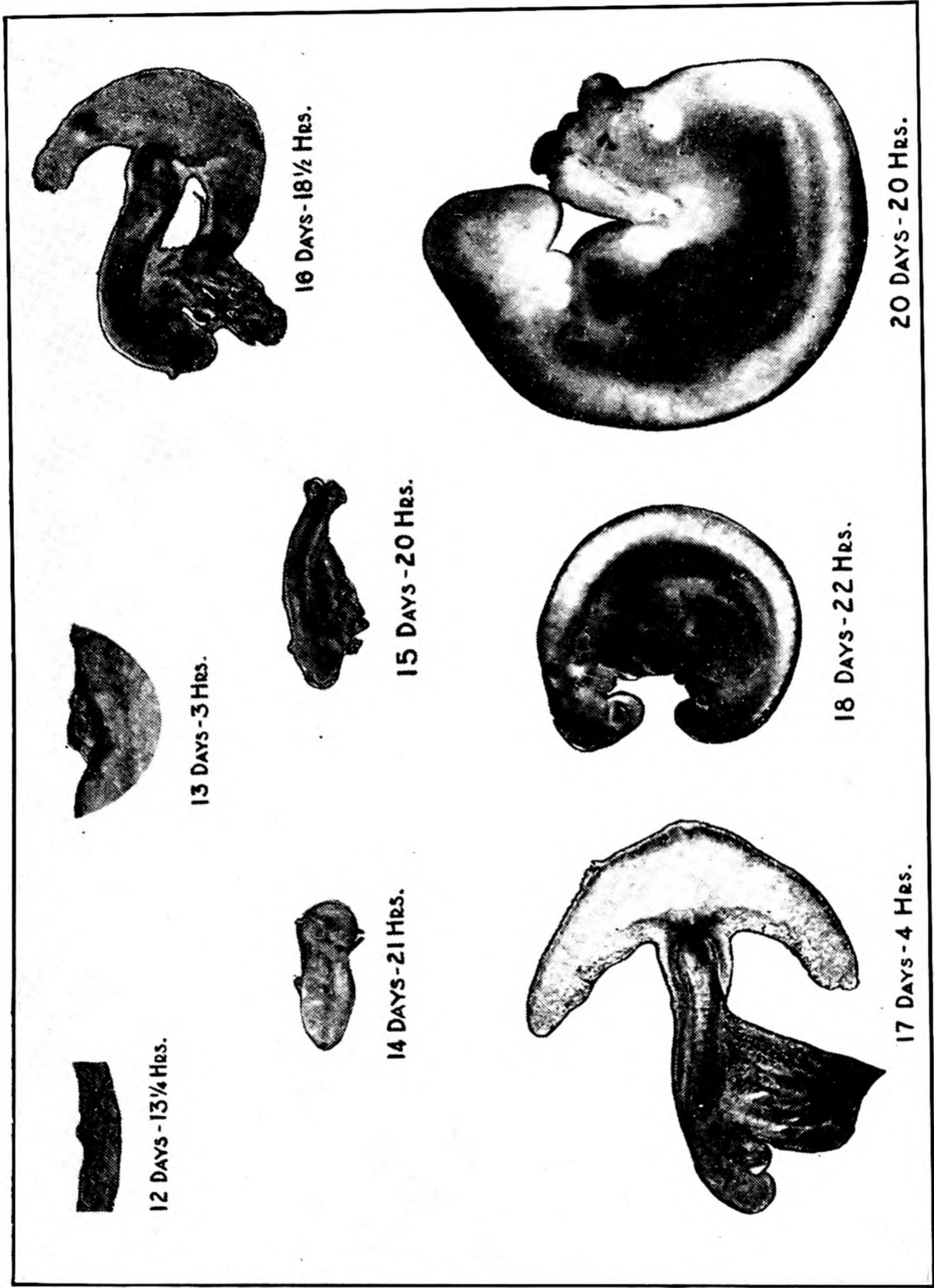
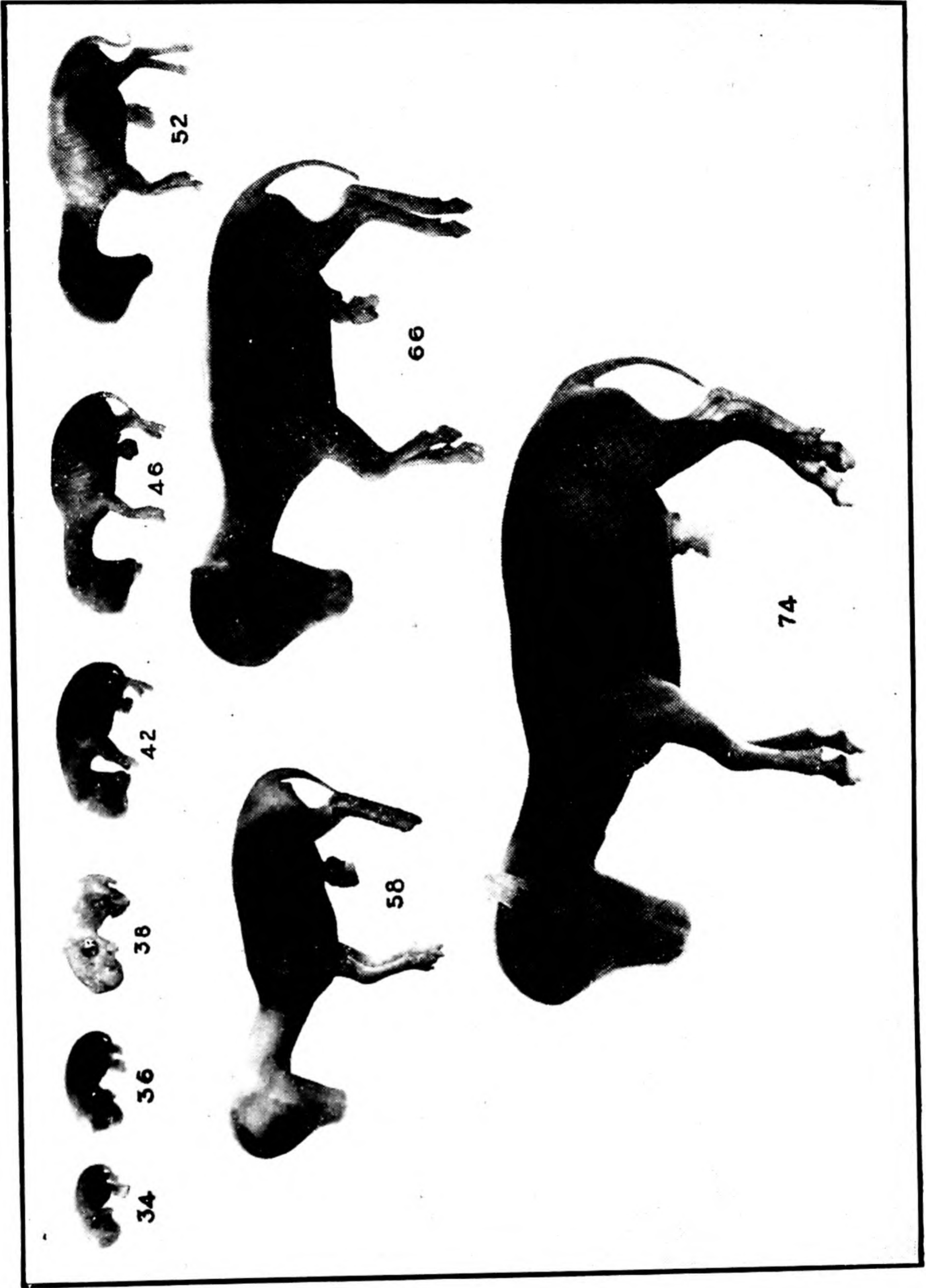
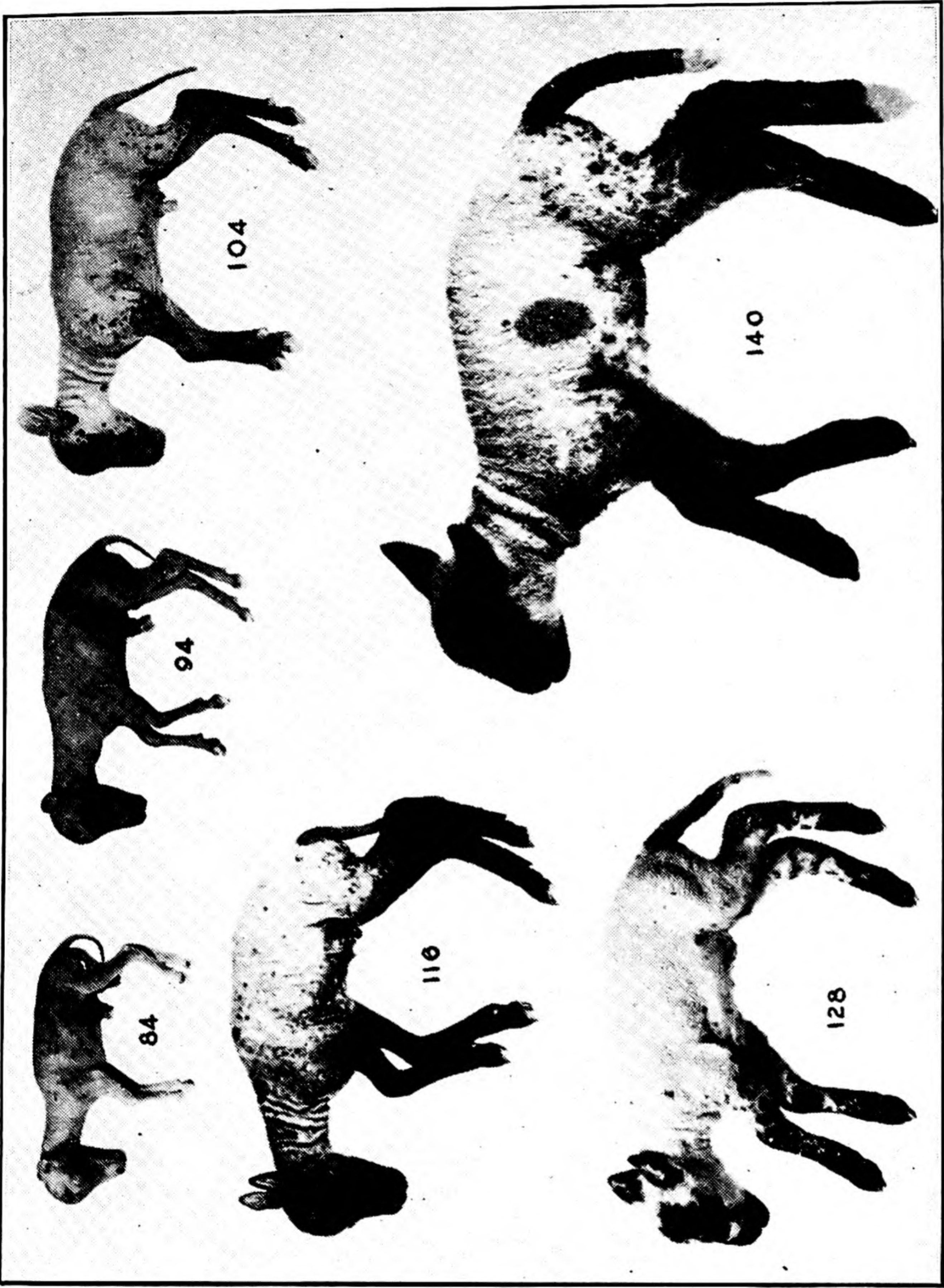


FIG. 28(b). The embryonic period in the sheep.



(c)



(d)

FIG. 28(c, d). The foetal period in the sheep. The specimens in 28(c) were all photographed at one magnification and those in 28(d) at another magnification. The ages in days are indicated by the numeral below each specimen.

Prenatal development is divided into three general periods: (1) the period of the ovum, (2) the embryonic period, and (3) the foetal period. The period of the ovum extends from fertilization until the segmenting egg becomes attached to the wall of the uterus. The embryonic period is that time when the organs and body parts are being formed. The foetal period is a period of general growth and a general reportioning of body parts.

Period of the Ovum. Segmentation of the egg follows fertilization and proceeds as the egg passes down the oviduct and horn. In the sheep and the bovine the first division is completed about 2 days after fertilization. It is impossible to be exact in timing growth during prenatal development because there is always the lack of certainty regarding the exact time of both ovulation and fertilization. The segmenting ovum does not become larger until the zona pellucida is lost some days later.

For some unknown reason the subsequent stages of segmentation are reached more rapidly than the two-cell stage. The four-cell stage is reached about 3 or 4 hours after the two-cell stage, and the eight-cell stage 2 to 4 hours later.

About 4 days are required for the egg to pass through the oviduct of the sow, the ewe, and the cow, and the eggs of all three species are in about the same stage of development (about the 16- to 32-cell stage) at the time of reaching the horn of the uterus.

In the sheep and the bovine the zona is lost about the beginning of the seventh day after ovulation. At this time the egg is well segmented and is in what is known as the trophoblast stage. The zona of the newly ovulated egg is rather viscous. The zona disappears as the egg ages, and shortly before it disappears it is quite brittle. It appears that the zona is lost mainly by shattering.

It has never been made clear whether the developing egg receives nutrient from the mother previous to attachment. It appears that the segmenting egg may get along very nicely on its own reserve cytoplasm until the zona is lost. After that it appears logical that the free trophoblast may pick up nutrients from the secretions within the uterus of its dam.

Implantation, attachment of the developing ovum to the wall of the uterus, occurs in the sheep sometime during the tenth or

eleventh day. In the bovine it occurs about 12 days after heat has passed, but since ovulation occurs after heat has passed in the bovine, the actual age of the new individuals is about the same in the two species. In the sheep and the bovine the first step in implantation is a sticking or gluing of the embryo to the wall of the uterus.

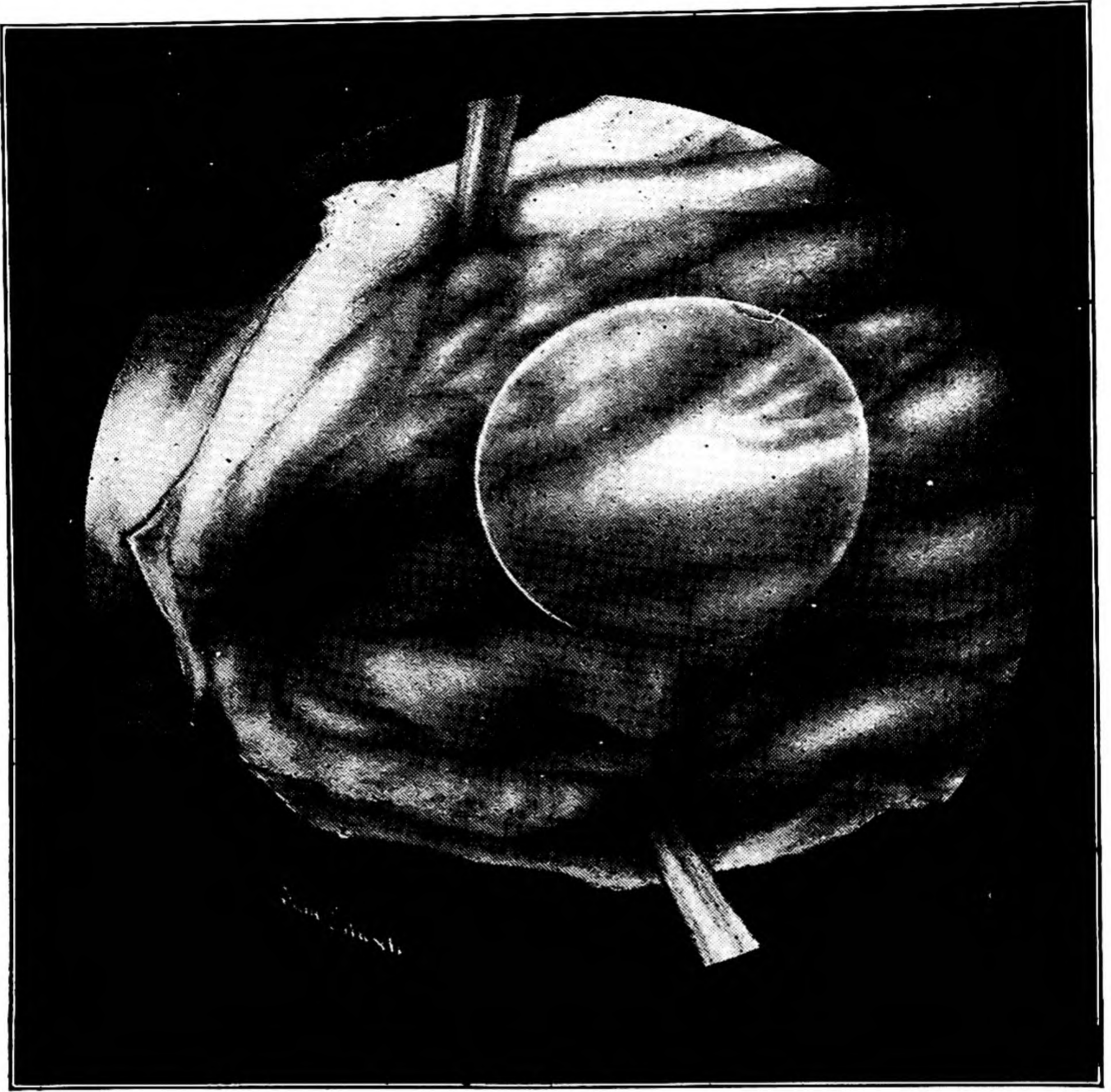


FIG. 29. Rabbit ovum ready for implantation. The uterus was laid open.

Importance of Understanding Prenatal Development. The student of animal breeding will do well at this point to spend considerable time studying the accompanying figures illustrating prenatal development. The student who fully appreciates how the new individual comes into being has a much better background with which to understand the significance of the applications of genetics; furthermore he is in a better position to appreciate the relative importance environment plays in animal

breeding. The reproductive organs of the dam provide the environment for the new individual for the first portion of its life. The prenatal period may constitute one-third or more of the total

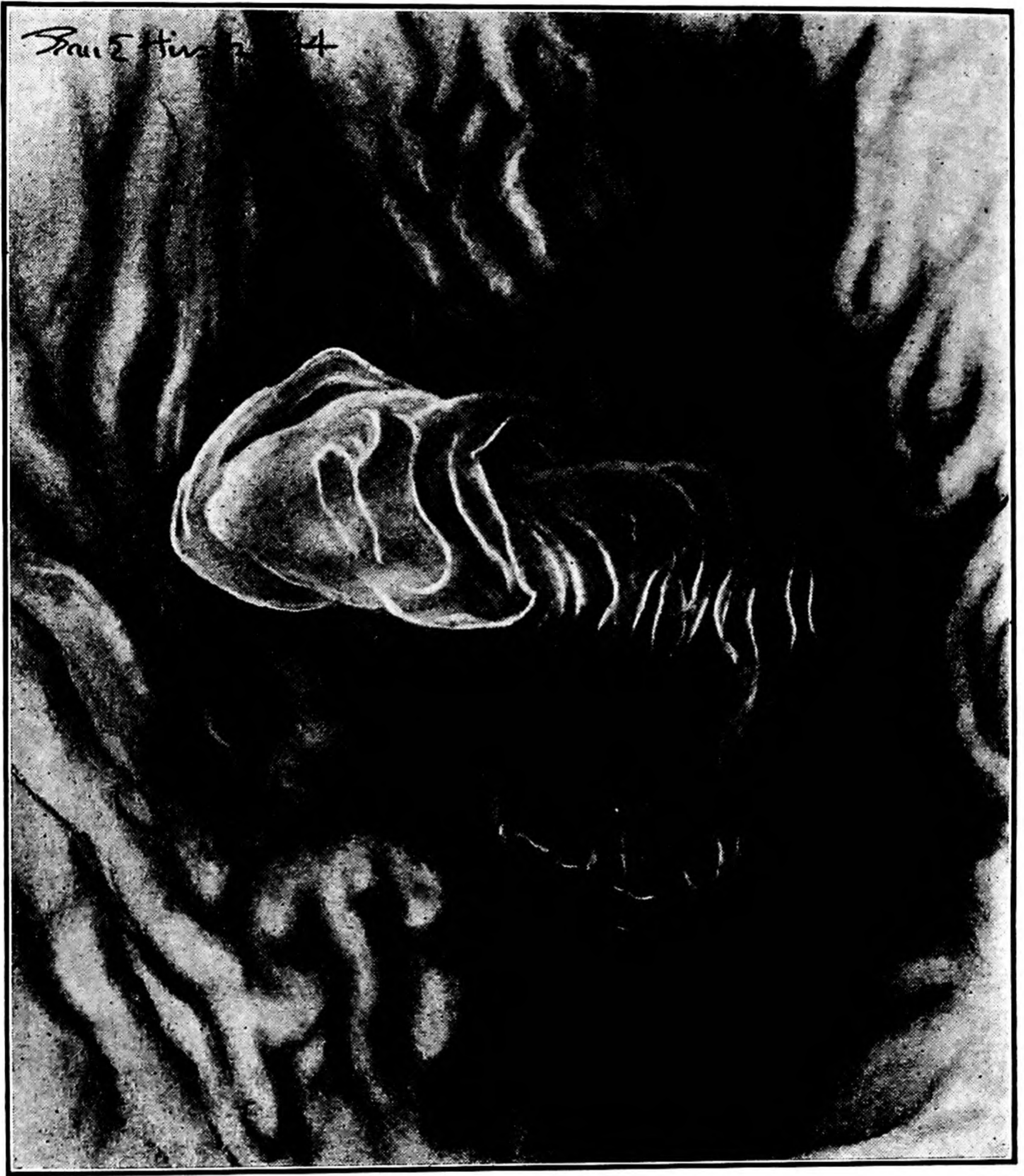


FIG. 30. Freshly implanted ovum of the pig.

life of modern market animals. Hence the heredity and the environment of the dam provide the environment for the new individual during its early life.

Foetal Membranes. The first task of the embryo after implantation is the development of the extra-embryonic membranes. The embryo must have food in order to grow. The dam's blood

supply is the food source; hence a communication must be established. Three membranes are developed: the allantois, the amnion, and the serosa.

The allantois is essentially an outpocketing of the hind gut. As such it enlarges until it comes in contact with the serosa, the outermost layer of the three foetal membranes. The allan-

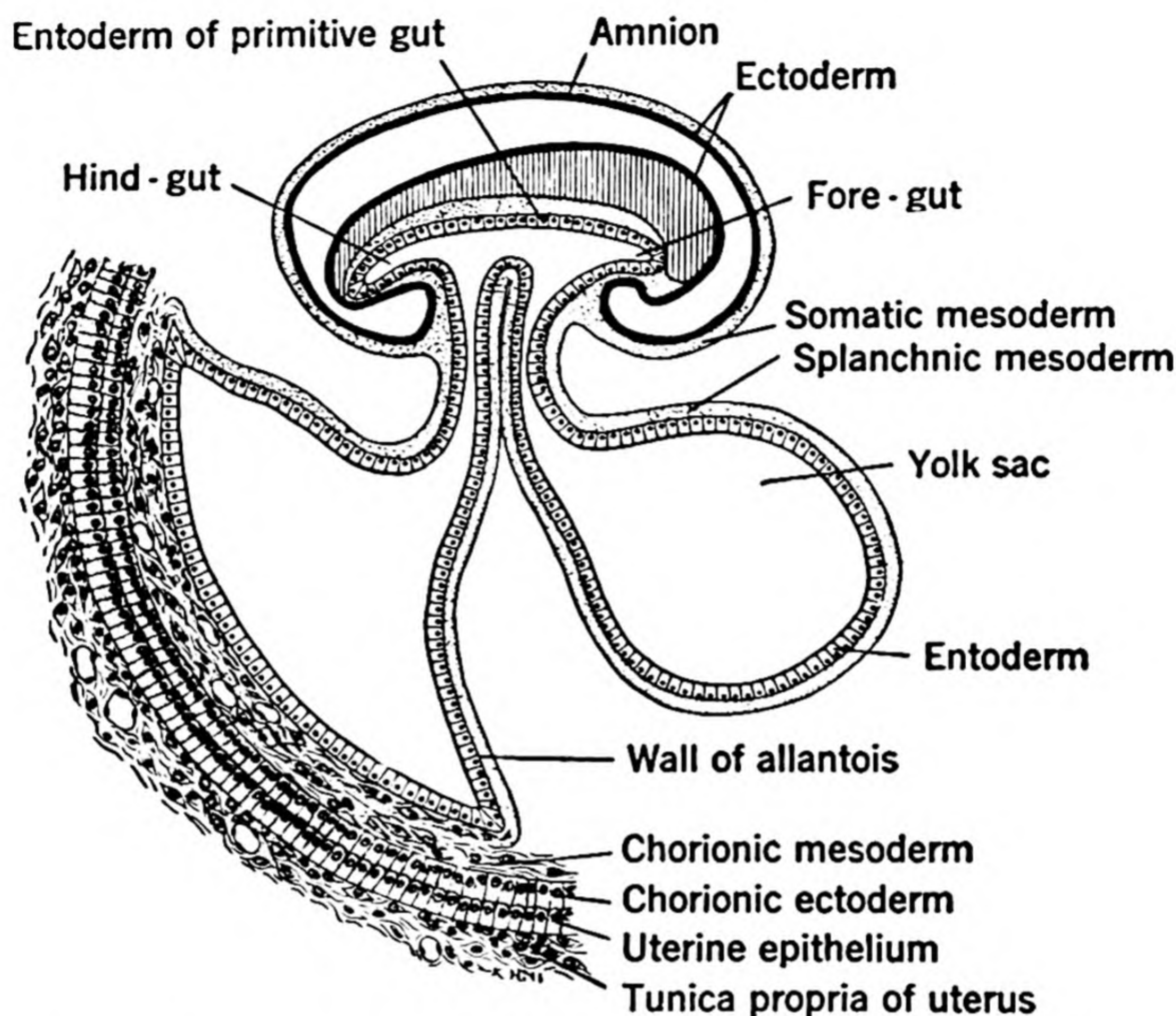


FIG. 31. Illustrating foetal membranes and attachments in the pig. (From Arey, *Developmental Anatomy*.)

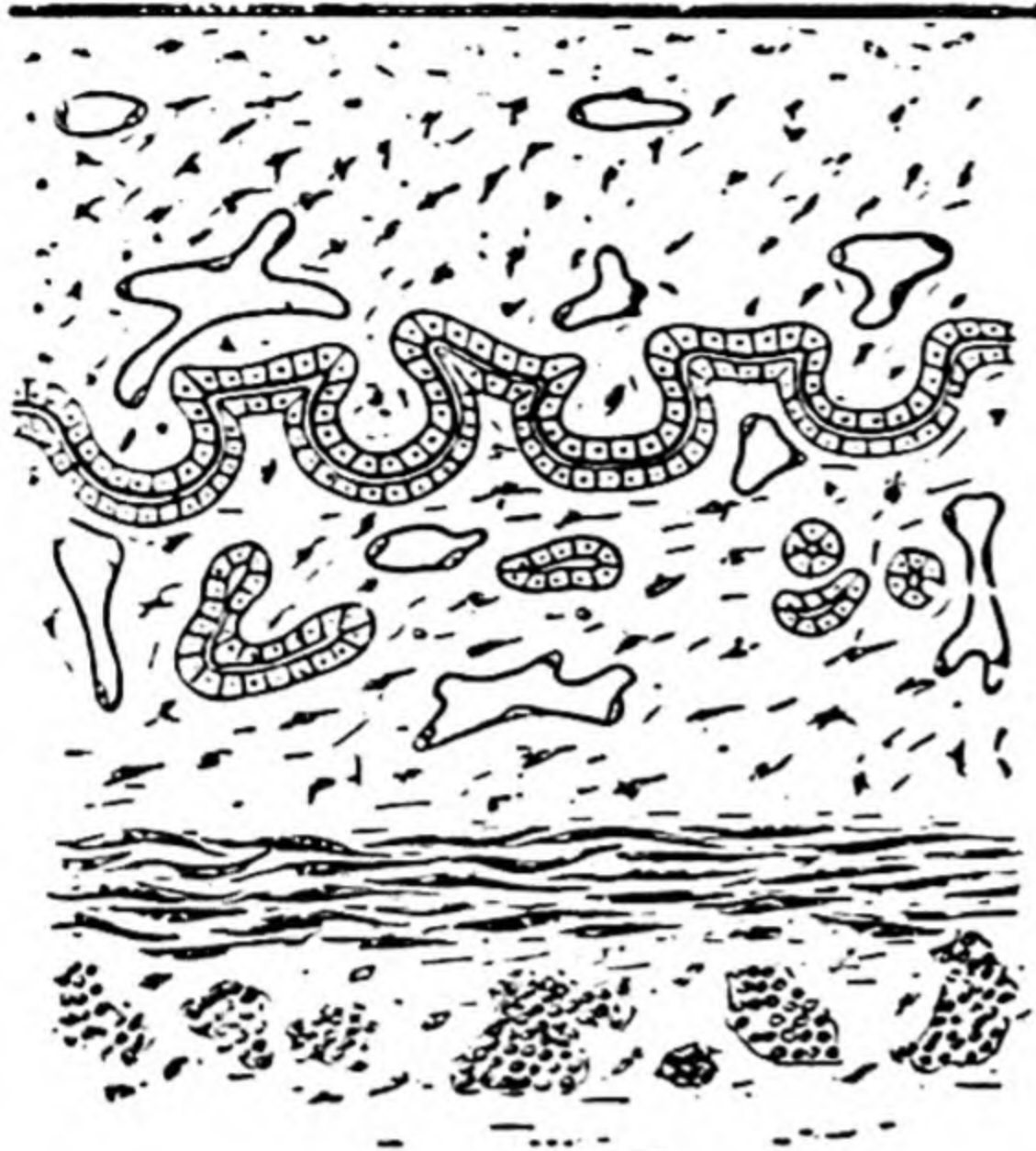
tois quickly develops an abundant blood supply which becomes the means of carrying food to the embryo and of carrying waste products from the embryo.

The amnion is the membrane which enfolds the embryo. The amniotic sac becomes filled with a watery fluid. The embryo is suspended in the amniotic fluid, which thereby equalizes the pressure about it and thus protects it from mechanical injury. It is also assumed that the soft tissues of the embryo are protected from adhesions and consequent malformations by being thus bathed in fluid.

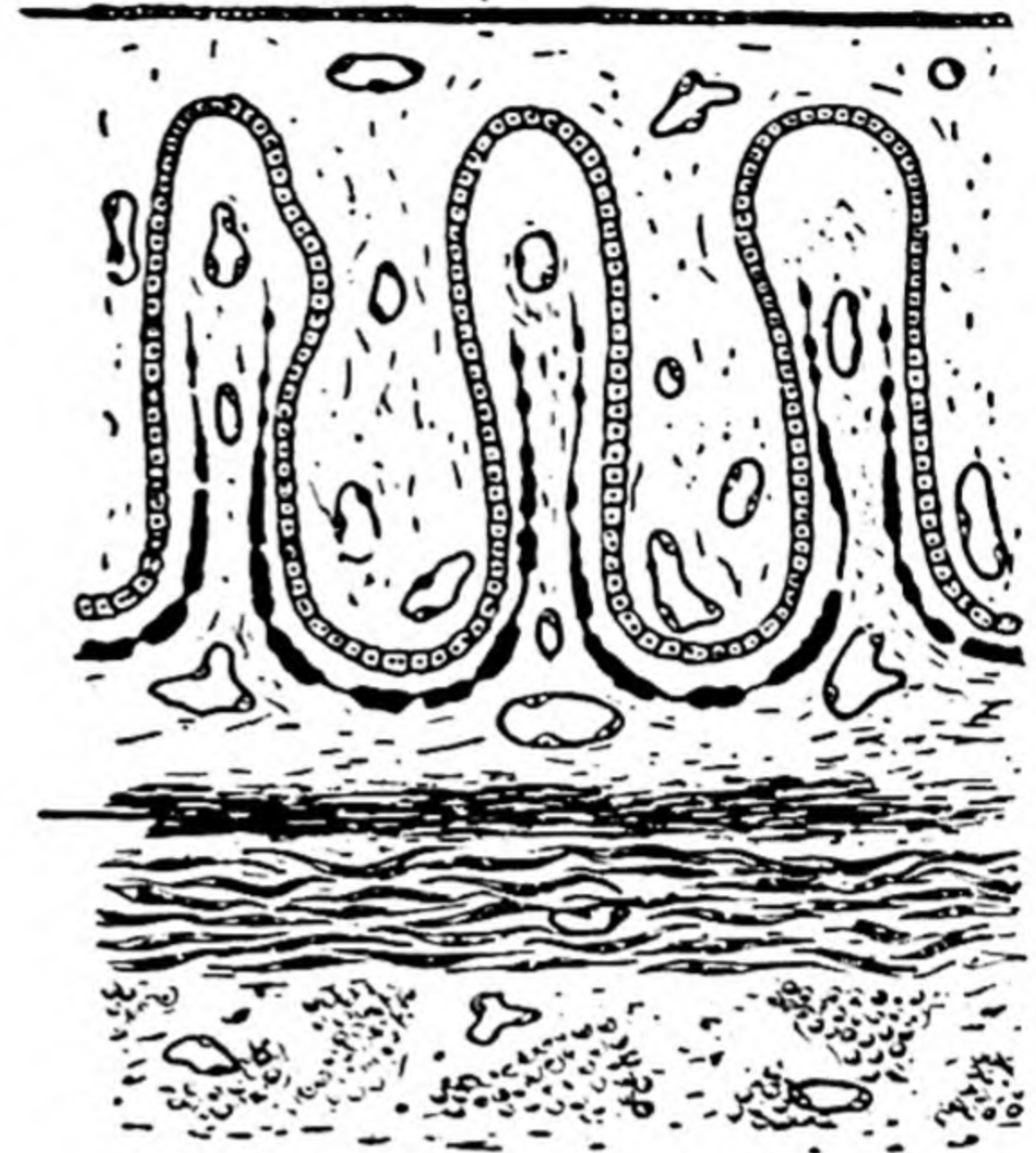
The serosa is the outermost layer of the foetal membranes. Its chief function is to establish contact with the uterus. In a

certain area or areas, depending on the species, the allantois fuses with the serosa to form the chorion.

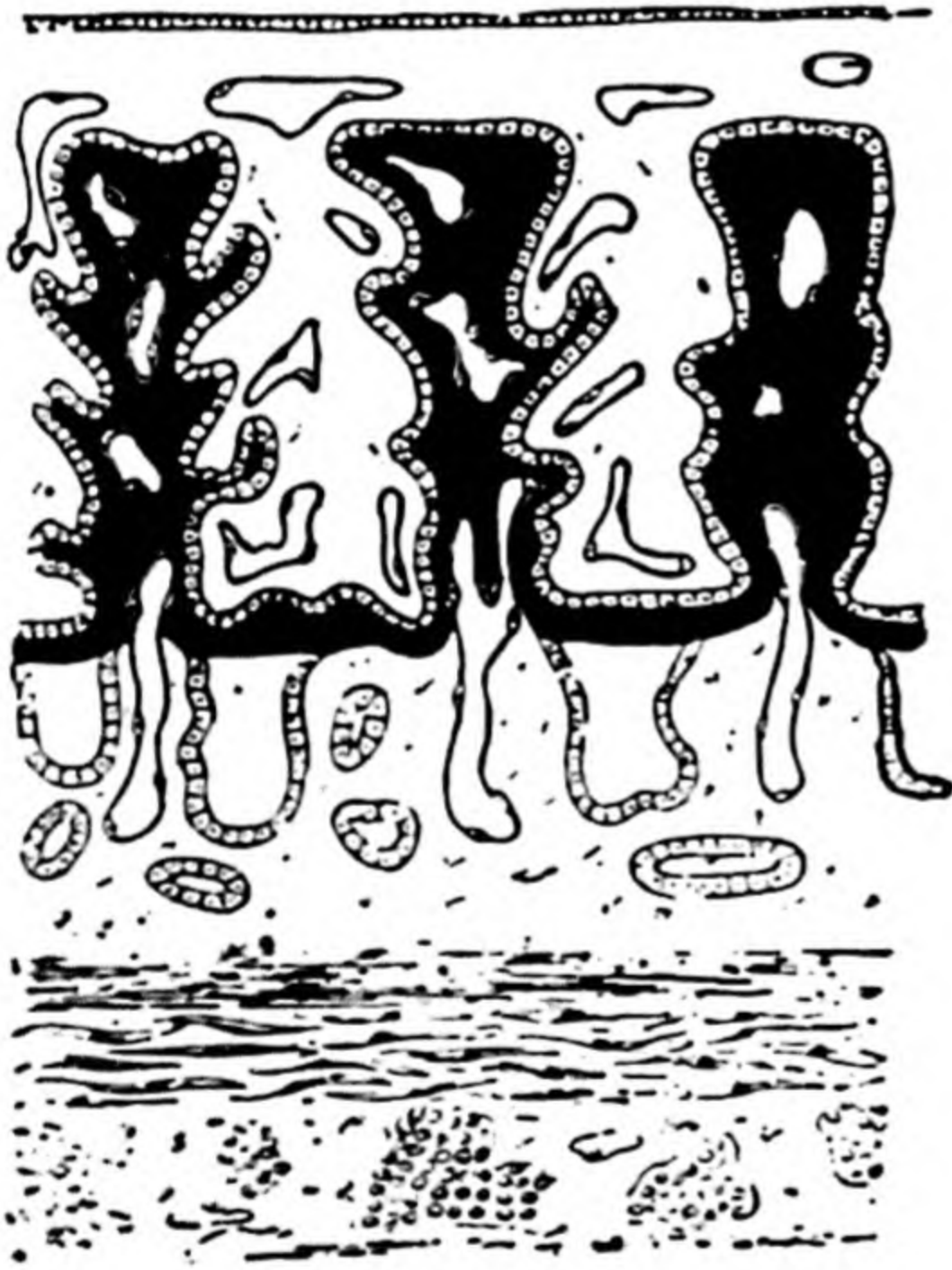
The chorion and the uterine mucosa make contact and together form the placenta. The placenta is therefore in part



a



b



c



d

FIG. 32. Illustrating different types of placenta: (a) the pig, (b) the sheep, (c) the cat, (d) the guinea-pig. (From Barclay, Franklin, Pritchard, *The Foetal Circulation*.)

foetal and in part maternal. Placental types vary with species. In the pig and the horse the chorion and the uterine mucosa come in close contact through a diffuse arrangement of chorionic villi. This is known as the diffuse type of placenta.

The ruminants, cattle and sheep, have the cotyledonary type of placenta. In this type the chorionic villi dip into the uterine glands. The intimate contact is made in a number of small areas known as cotyledons. This type of placenta is regarded as more efficient than the diffuse type but less efficient than the deciduate type of the carnivora. In the deciduate type the contact between foetus and mother is much more intimate; there is an actual erosion of the uterine mucosa. It is assumed that the erosion is effected by ferments liberated in the chorionic epithelium. In primates and rodents the erosion of the uterine mucosa results in the opening of the maternal blood channels; the chorionic villi are bathed in maternal blood.

In all types of placenta the result is the effecting of a means of vascular contact between foetus and mother.

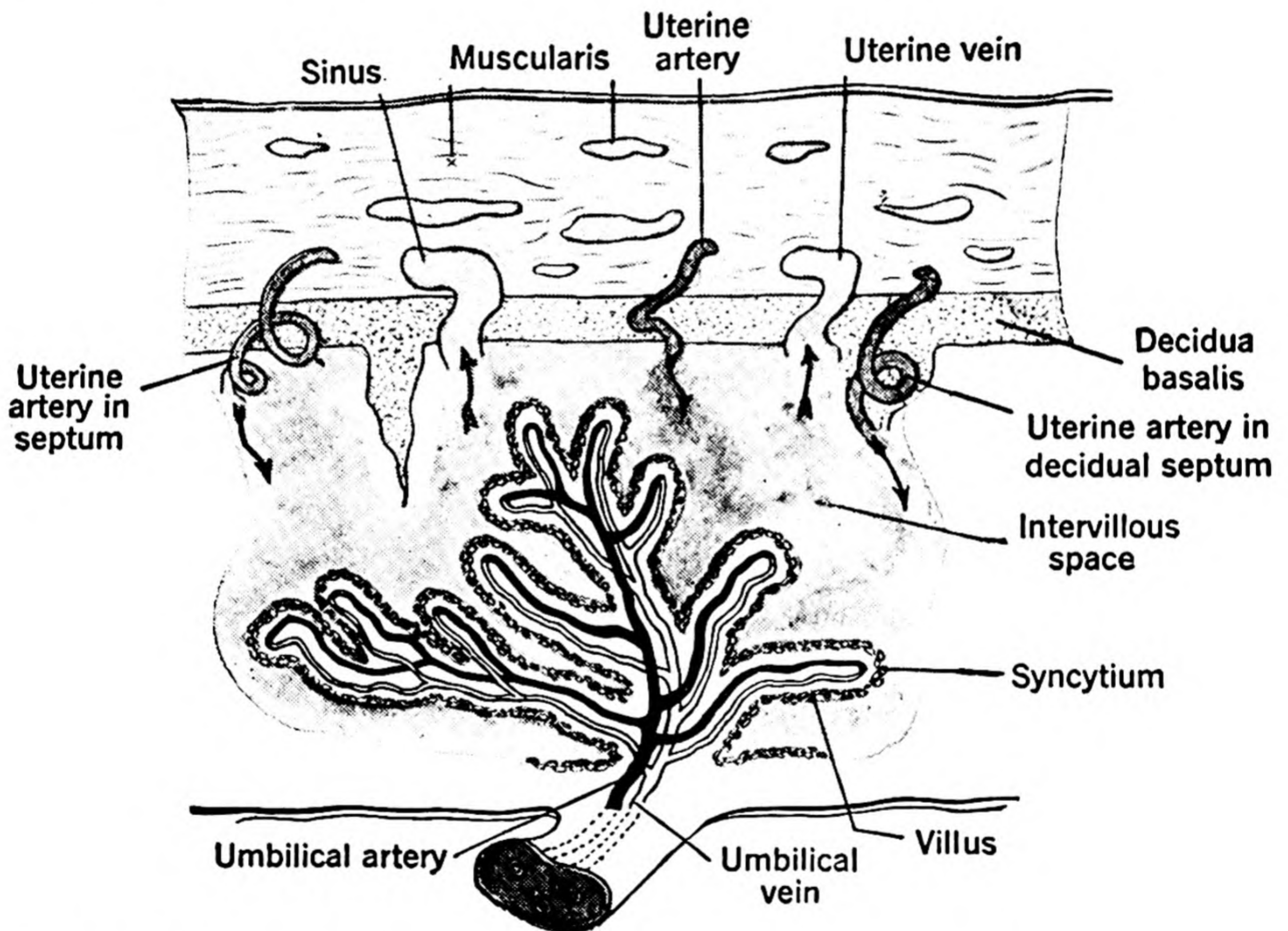


FIG. 33. Illustrating the vascular contact between dam and foetus. (From Arey, *Developmental Anatomy*.)

Embryonic Period. The embryonic period in the sheep extends from the tenth or eleventh day to about the thirty-fourth day. In the bovine it extends from about the eleventh day to the forty-fifth day. This is the period during which the body

organs are laid down. It is a period of rapid change and rapid growth.

The embryonic period is a very important one in the life of the individual. One misplaced cell at this time may lead to a serious malformation. The fundamental means by which the many body organs and their tissues are formed are little understood. It seems odd that each of the many, many highly differentiated body cells should carry the same component number of chromosomes and genes as the original fertilized egg, and yet that is our present understanding of the situation. It appears that the differentiation of tissues and body parts is effected through the reaction of the genes and their environment. In this case the environment is provided by the tissues and their secretions, both of which are products of the original fertilized egg. Here indeed is one of nature's great phenomena; yet it is occurring so regularly in our daily lives that an occasional malformation is often looked on as very strange. The student of animal breeding will do well to pause at this point and meditate on the remarkable precision with which all the many details of organology are carried out, for through pondering he should widen his perspective of the mechanisms involved.

The Foetal Period. This is the period of growth. In the sheep it extends from about the thirty-fourth day to the one hundred forty-second to one hundred forty-eighth day, and in the bovine it extends from about the forty-fifth to the two hundred eightieth day. During this period the ratio of size of body parts changes markedly. The head, liver, and heart, for instance, are much larger during early foetal life than later.

Foetal Nutrition. The total amount of dry matter present in the newborn animal is very small, but, nevertheless, it is very important because only a slight reduction in amount or proportion may make the difference between life and death.

Verges (1939) found that when ewes were kept at constant weight, through controlled feed intake, during the latter half of pregnancy, the twin lambs weighed only 6 pounds at birth, whereas ewes fed to gain 39 pounds during this period produced lambs that averaged 9 pounds.

Murlin (1916) studied metabolism in the bitch during two consecutive pregnancies in which one pup was produced at the first and five pups at the second birth. Increased caloric energy

production due to the single foetus was detected at the sixth week. Between the sixth and eighth weeks it amounted to 9 per cent. At full term the total energy produced was proportional to the weight of the offspring, and it was about equal to that required by the newborn pups. Birth caused no deflection in the curve of total energy production of the bitch and her pups. It is extremely interesting that the number of calories produced by the resting pregnant bitch and her foetuses and foetal membranes was about the same as that produced after parturition by the lactating bitch and her resting pups.

The necessity for an adequate supply of amino acids, vitamins, and minerals appears to be even more important to the developing foetus than the total plane of nutrition.

It is well recognized by practical stockmen that the vigorous well-developed newborn is more likely to survive and thrive than the individual that is less well-born. The would-be constructive breeder is, therefore, well advised to give careful consideration to the environment of the young previous to birth.

The Rôle of Heredity

Everyone believes in heredity although he may not always recognize the completeness of his belief. As a simple illustration, it is well known and recognized that offspring tend to resemble their parents; for example, a Hereford cow bred to a Hereford bull will produce a Hereford calf. The control exercised by inheritance over the animal's development and life itself is very broad, so broad that much of its control is overlooked. Not only is there a resemblance between related individuals but there is a uniformity in the appearance and development of characters. In sheep, for example, the lamb's teeth are all present the first year; in the shearling, the center incisors are replaced by two permanent ones; in the two-shear, the second pair are replaced; in the three-shear, the third pair; and as a four-year-old the sheep exhibits a full mouth. In horses and in cattle still different timings are followed in the replacement of teeth.

One of the best illustrations of the complete domination of an organism by heredity is to be found in comparative embryology. Here the evidence is so overwhelming that it is easily overlooked. The mammal, during prenatal life, more or less relives the lives of its ancestry; a close study of the figures illustrating prenatal development of sheep and bovine (Chapter VI) will show how the new individual passes through various stages bearing resemblances to the ancestral forms through which it is believed the mammal passed in its long journey of evolution. These resemblances become much more marked when the details of organology are studied. This is known as the theory of recapitulation. Recapitulation never establishes an identity between the embryonic stages of the higher forms and the adult stages of the lower forms. The imprint of the earlier ancestral structures are left but they are modified somewhat or covered by the acquisition of new characters which have been added through the many, many generations of evolution.

The above analogy may be illustrated by the following: the fertilized egg may be compared to a single-celled protozoan such as the amoeba; the 32-cell stage to a protozoan such as the flagellate; the blastula stage, about the time the zona pellucida is lost, to a form like the Volvox; and the gastrula stage, the egg at about the time of implantation, to one of the sponges. The elongated stage that follows implantation may be compared to a simple flatworm; shortly after this the body form becomes somewhat like that of the Amphioxies. The analogy may be carried much farther, but doing so leads to a study of comparative embryology.

Hammond (1940) has extended the theory of recapitulation to encompass the evolutionary changes made during domestication and the improvement of animals by breeding. Furthermore, he has made practical interpretations from this fundamental law of biology. Hammond points out not only that the modern farm animal relives the lives of his remote ancestors but also that he passes through the body form of his not too distant ancestors. Note the similarity in body form and proportions of the 4-day old Suffolk

lamb and the adult unimproved Mouflon (Fig. 6). Note also the general similarity in body outline and proportions between the newborn pig and the adult wild boar (Fig. 34). Hammond contends that in the hands of man the process of body development has been speeded up markedly and this speeding up of

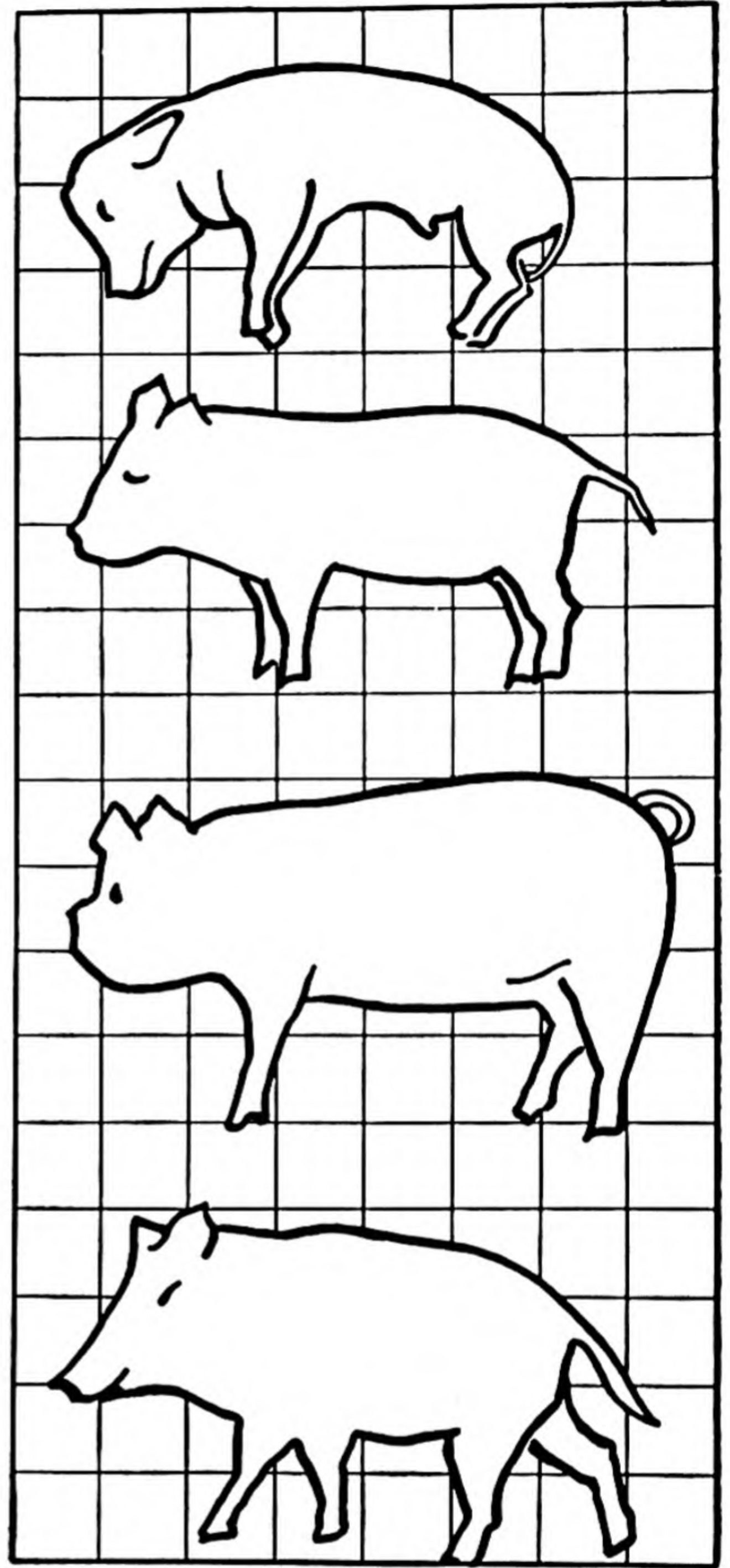


FIG. 34. Illustrating the evolution in body form of the pig. Note the similarity in general outline of the young pig of today and that of the wild boar. (After Hammond.)

development has especially effected an increased proportion of the formerly late-developing parts.

Hammond presents data from McMeekan to show that, as the plane of nutrition is increased, there is a corresponding in-

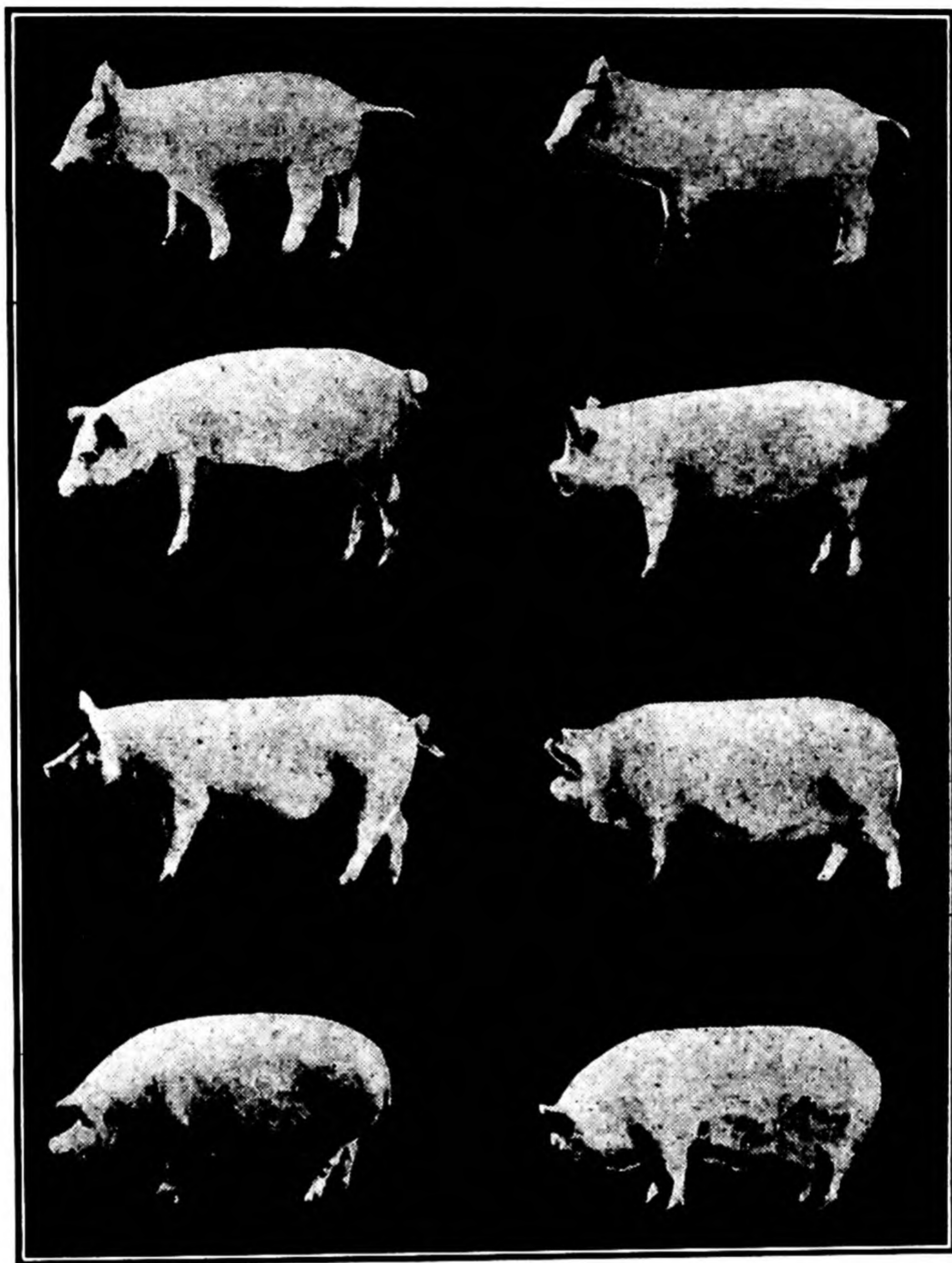


FIG. 35. Illustrating changes in body proportions of the pig as it grows up. Right, the England Middle White; left, the Large White. (From Hammond, *Farm Animals*.)

crease in the rate with which the animal passes through the evolutionary changes of form and proportions (Fig. 35). According to Hammond the head is one of the early-developing body parts whereas the loin lags in development. Through an increased plane of nutrition the ratio of body parts has been changed markedly. Hammond then makes this very practical deduction “. . . unless the pig is put on high-plane nutrition and has a good growth rate the full commercial qualities of the breed

cannot be exploited nor can the capabilities of the animal for producing a high proportion of loin to head be determined and so proper selection of breeding stock be made."

The above discussion has led the reader somewhat beyond the scope of this chapter and into that of later chapters. The purpose was, however, to give the student of animal breeding a bird's-eye view of the many ramifications of heredity beyond the details of single gene effects.

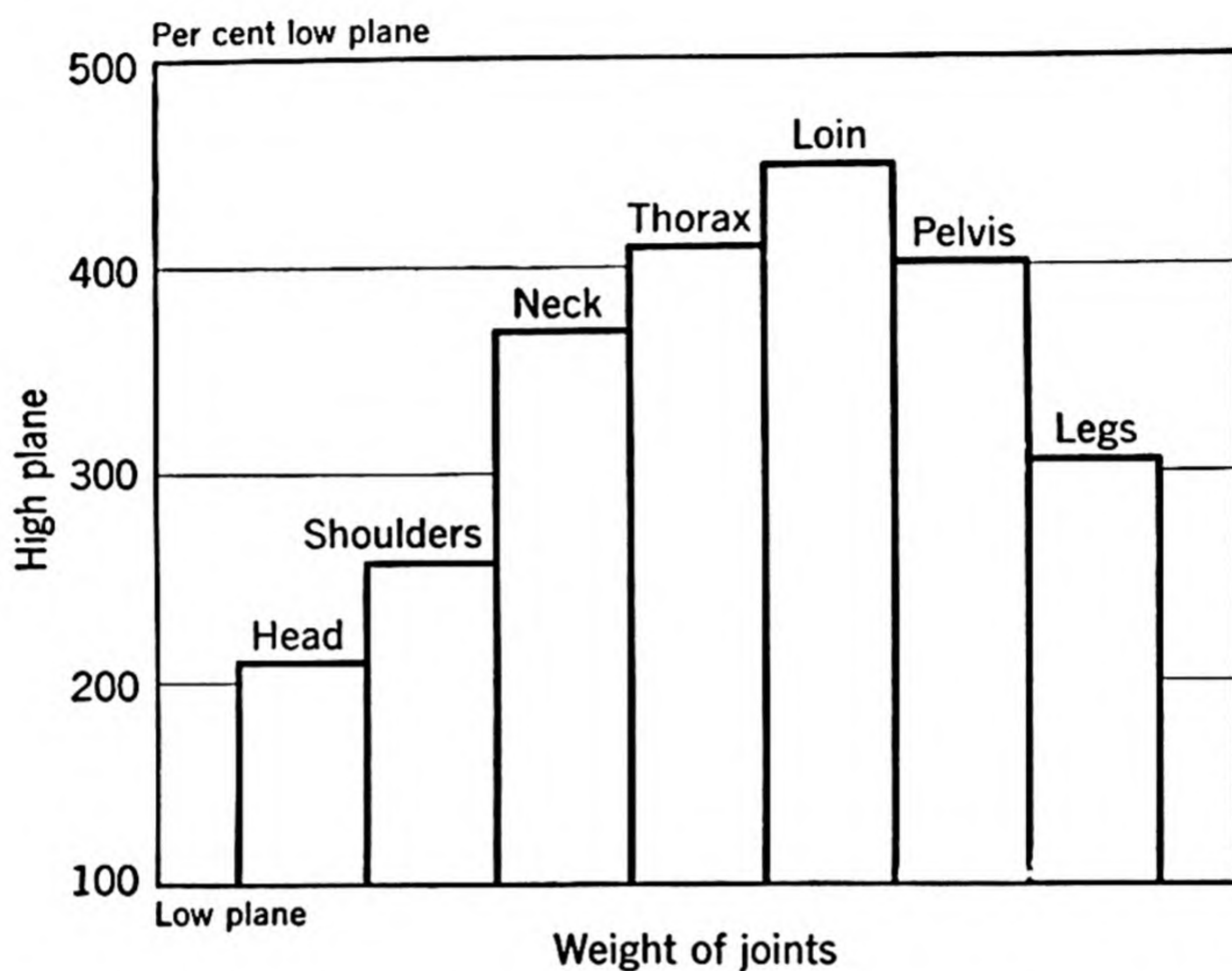


FIG. 36. Illustrating differences in body proportions of pigs at 16 weeks that had been fed on high and low planes of nutrition. The weight of the body part of the high-plane pigs is shown as a percentage of the weight in the low plane. (From Hammond, *Farm Animals*.)

The laws of inheritance not only seek to account for the resemblance of related individuals but also recognize and seek to explain the lack of similarity between related individuals. Heredity, however, does not need to account for all the resemblances of related individuals. The association of offspring with their parents is an important factor affecting the offspring's traits. Range cattle shifted to confinement tend to raise wild calves like themselves. That heredity is the only governing factor in this case is unlikely; rather, the association of the calves with their dams who are nervous and high strung because of previous environmental influences is the important factor. We, therefore, need to exercise a certain care in accounting for the

similarities of related individuals because environment, even to the point of similar food, as well as heredity plays an important part in bringing about similarities and likewise variations.

Heredity and Environment. The individual's ultimate attainment in life is determined by both heredity and environment, and a deficiency in either will interfere with maximum attainment. Figure 1 illustrates a five-day-old Hackney foal showing remarkable action. This is the result of its inheritance, for environment has not yet had the opportunity to exert any appreciable effect. Eventually environment may play an important rôle in bringing out certain refinements of action so that the foal may develop into a future prize winner. It is perfectly clear, however, that the foal's inheritance has already circumscribed its possibilities; for instance, no environment can so affect this foal that it will develop into either a race horse or a draft horse.

A satisfactory picture of the interworkings of heredity and environment may be obtained if we visualize heredity as circumscribing an individual's future attainments, mental and physical, as well as morphological. This is illustrated in Fig. 3; the outer circle represents the hereditary limits of the individual's possibilities at the time of fertilization. The small dot represents its attainments at that time. Whether the individual ultimately fills the circle depends on its future environment, but regardless of its environment it cannot go beyond the bounds of its heredity.

Heredity, therefore, is fundamental and may be thought of as furnishing the foundation, with environment completing the structure. Hence, another method of illustrating the interrelationship between heredity and environment, therefore, is to think of heredity as the foundation of a building. The type and size of the foundation place very definite limitations on the type and size of building that may be constructed, but it does not guarantee that a building of a certain type and size will be built.

The above illustrations of the relationship of heredity and environment are correct in the abstract, but in actual operation the individual is the result of the interworking of heredity and environment. Each affects the outcome of the other.

Lush, Hetzer, and Culbertson (1934) studied the relative effects of environment and heredity on the birth weight of pigs. Their

findings were that only 6 per cent of the variance in weight at birth was due to the heredity of the pigs. Environment common to litter mates was responsible for 47 per cent, and environment not common to litter mates was responsible for the remaining 47 per cent. Of the 47 per cent due to environment common to litter mates, litter size is credited with 7 per cent, year with 5 per cent, ration 4 per cent, length of gestation 2 per cent, and other causes 29 per cent. The heredity of the dams undoubtedly is one of the important factors that cause the other 29 per cent.

Wright (1920) made one of the first careful analyses of the relative importance of heredity and environment, in a study of the amount of white spotting in guinea pigs. One of the stocks used for analysis had been inbred by brother-and-sister matings for more than ten years; hence it should have been highly purified. The other stock was an outbred one. Careful analysis showed that the amounts of variance due to environment in the two populations were about the same, 0.354 in the inbreds and 0.372 in the outbreds; but environment was the cause of 97.2 per cent of the variance in the inbred stock and the cause of 57.8 per cent of that in the outbred stock.

The above is a very good illustration of a character that lends itself to accurate measurement, but one that would not be considered subject to that much environmental influence.

Detailed pursuance of the above and its applications will be found in later chapters, chiefly Chapters XI and XII. The purpose of introducing the subject at this point is to widen the viewpoint of the student before he becomes engrossed in the details of inheritance.

Every organism becomes what it becomes as the result of its inheritance and its environment. A serious deficiency in either one will result in an organism that is a failure. Since an organism cannot develop beyond the limits set by its inheritance and since a proper environment is necessary in order that an organism may expand to the limits set by its inheritance, it is essential that the breeder who wishes to produce animals to the best advantage should supply his animals with as desirable an inheritance as possible, and as desirable an environment as is in keeping with sound economy. The truly constructive breeder should, however, rear his animals in an environment that is as similar as possible

to that under which the commercial descendants of his stock are to be produced.

Maternal Influences. The actual genetic contributions of the two parents are equal (ignoring, for the time being, differences in the X and Y chromosomes involved in sex determination), yet the direct effect of the mother may be greater than that of the father on the offspring's development. This is due to the fact that the mother furnishes the environment for the offspring from conception until birth and usually contributes materially to the environment from birth until weaning. A classic example of this is furnished in the reciprocal crosses of Shire and Shetland horses by Hammond (1940). At birth the crossbred foal out of the Shire mare weighed three times as much as its reciprocal mate and at four years old it still weighed one-and-a-half as much as the foal out of the Shetland mare. The crossbreeding studies of swine by Winters *et al.* (1935), reported on page 248, show that crossbred sows, owing to their own greater vigor, contribute about as much increased performance to the offspring as the increase in vigor of the pigs due to their own crossbred state. So far as the young are concerned, the increased performance due to maternal influence is environmental and not hereditary.

Control of Heredity. The livestock breeder's aim is to gain a maximum control over heredity. His ambition in breeding for improvement is to exercise such control that in future generations only the most desirable characters may be perpetuated and the undesirable may be eliminated. However, if one considers that the determiners of the future animal's various characters are wrapped up in probably thousands of genes, the genes in some 40 to 60 chromosomes, and the chromosomes in cells from $1/125,000$ to $1/125$ of an inch in diameter, one can appreciate how extremely difficult and even unlikely will be the control of heredity through the manipulation of these innumerable details.

The control of heredity in animal breeding is, however, far from hopeless. The two germ cells that unite to produce the new individual arise from the individual's parents, and it is by means of them that the individual inherits all its anatomical, physiological, and psychological characters. A more complete understanding of the parents' genotypes gives the breeder something more tangible to work with than concentration on phenotype. It is possible to obtain a better understanding of the

individual's genotype through the development of groups of individuals that possess a high intrarelationship and a strong similarity both phenotypically and genotypically. (This too is discussed more fully in the following chapters.) The genotype of the individual and his near relatives becomes more completely revealed when they are reared under a more completely controlled environment and in an environment designed to bring forth both the traits desired to be perpetuated and those desired to be eliminated.

The above does not, however, eliminate the need for increased knowledge and appreciation of the many details of inheritance. An appreciation of these details will enable the breeder to approach his task more intelligently.

CHAPTER VIII

Fundamental Mendelism and Animal Breeding

Gregor Johann Mendel, an Austrian monk and teacher of the physical and natural sciences in a monastic school at Brunn, Austria, laid the foundation for an understanding of the laws of heredity. Brief accounts of his work were published in 1866 in the proceedings of a local scientific society; they remained unheeded until rediscovered simultaneously thirty-four years later by Tschermak of Austria, de Vries of Holland, and Correns of Germany.

For eight years, by the crossbreeding of peas, Mendel made a series of hereditary studies regarding the behavior of contrasted characters. From these studies, he drew some conclusions, now known as Mendel's laws of heredity, which deal with the inheritance of contrasted or allelomorphic characters. The work, although carried on with peas, has been confirmed as basic to the whole problem of inheritance.

Mendel's Objective. Mendel's close observations of crossbreeding led him to believe that certain ancestral characters reappeared with a definite numerical regularity when the hybrids of the first, second, and succeeding generations, respectively, were interbred. He, therefore, set out (1) to ascertain, if possible, the number of different forms under which the offspring appear, (2) to arrange these different forms with certainty according to their separate generations, and (3) to ascertain definitely their mutual numerical relationship.

As the result of this work, Mendel in reality laid down what have become two laws or fundamental principles of heredity: (1) the law of segregation, and (2) the law of independent assortment.

In addition to establishing the above-mentioned laws, Mendel initiated the use of exact experimental methods in the study of

the problems of heredity. At the time of Mendel and during the period in which his work remained unrecognized the problems of heredity were being approached usually through generalizations. A notable exception to this was the evidence Weismann gathered contradicting belief in the inheritance of "acquired" characters. Weismann also identified the nuclei of the gametes as the material basis of heredity.

The Law of Segregation. If a pure polled bull is crossed with horned cows (or vice versa), the resulting hybrids are not midway between the two parents; they always possess the polled character. Characters that are transmitted entirely or almost unchanged in the hybridization, such as the polled character, are termed dominant characters; those that recede from view, such as the horned character, are termed recessive characters.

Dominance, therefore, is a property possessed by certain characters, by virtue of which, when individuals possessing allelomorphic characters are interbred, all the resulting offspring in the first (F_1) generation will exhibit the dominant character; that is, when pure polled and horned cattle are crossed, all the hybrids will exhibit the polled character, since it is dominant to the horned character.

When these hybrids are interbred, the recessive (horned), as well as the dominant (polled), character will appear in the second (F_2) generation. Among large numbers they will appear in quite definite proportions, so that, on the average, among four individuals of the second generation three will exhibit the dominant character and one will receive the recessive character; that is, three polled individuals to one horned.

If the horned individuals of the F_2 generation are interbred, the resulting offspring will exhibit the horned character. On the other hand, if the polled individuals of the F_2 generation are interbred, they will continue to segregate. One-third of the polled individuals will breed true in regard to the polled character, whereas two-thirds will, like their F_1 parents, produce gametes one half of which carry the polled factor, and the other half the horned factor. In successive generations, segregation will continue as outlined above.

The law of segregation arises from the above results. It may be stated thus: Since the F_1 generation, when interbred, produces offspring in the 3 to 1 proportion, 3 polled to 1 horned,

it is clear that genes contributed by the two parents, each of which has a definite rôle in the determination and development of characters, separate in the germ plasm of the offspring without having influenced each other. This point was realized and pointed out very clearly by Mendel. It is a very significant fact, and it marks a sharp departure from Weismann's theory of

"amphimixis." It is also in marked contrast to the far too popular conception that an outcross introduces a hereditary contamination beyond repair and that genetic purity is achieved only through years and years of breeding to a given end and this is achieved without inbreeding.

The law of segregation may be more clearly understood by studying the accompanying diagram (Fig. 37). In this diagram, *P* denotes polled, the dominant character; *p*, horned, the recessive character; *Pp*, indicates that the phenotype is polled but breeds as a hybrid, producing both polled-

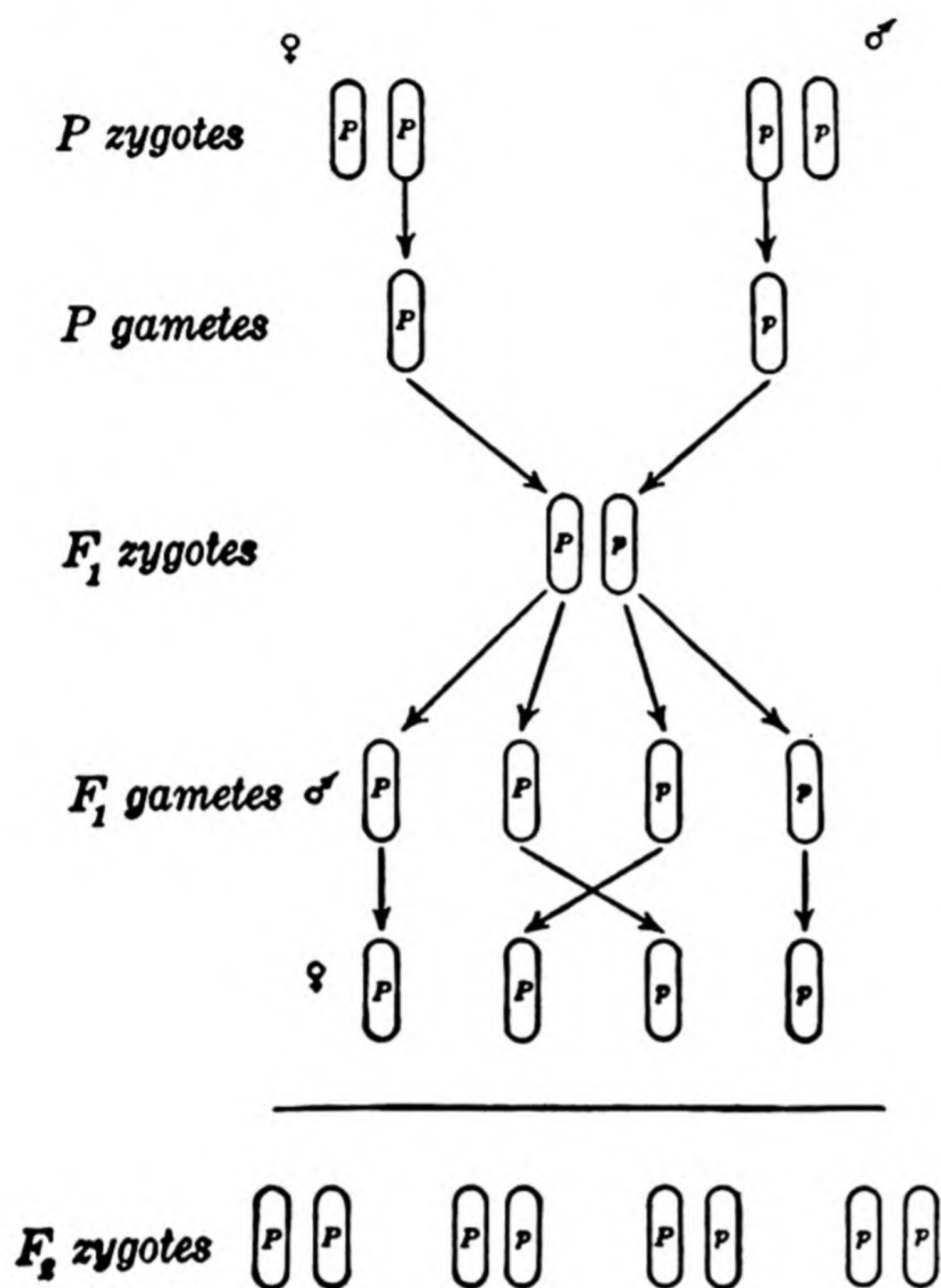


FIG. 37. Illustrating the combination and segregation of the factors for polled and horned in which *P* represents polled and *p*, horned.

and horned-producing germ cells; and *PP* and *pp* denote purity of breeding powers, each phenotype producing only one kind of germ cell. In the *F₂* population, therefore, there are three polled individuals to one horned. The horned animal will breed true because it has no *P* factors in its complex. Of the three polled individuals only one, the *PP* individual, will breed true; it possesses only *P* factors. The two other polled animals (*Pp*) will produce one germ cell carrying *P* to every one carrying *p*.

Black and red color in cattle behave similarly to polled and horned characters. Black is dominant to red; hence when a pure black is crossed with a pure red the offspring is black. The resulting black, however, is not pure for black, but will produce

germ cells one of which will carry black to one carrying red. The genetic constitution of the resulting black will be Bb ; B stands for the dominant black and b for the recessive red. When an F_1 bull is used on F_1 cows, the F_2 population will be, on the average, three black to one red. The red like the horned animal will be pure. Of the three blacks only one will be pure for black; its genetic constitution will be BB . The other two will be Bb in genetic constitution and will produce as many germ cells carrying b as germ cells carrying B .

It is, therefore, clear that a dominant character will cover up a recessive; hence an animal's breeding performance cannot be recognized from its phenotype, a fact of great significance in practical breeding. More emphasis is placed on this point later in this chapter and in the book. It is well, however, for the student of animal breeding not to be too hasty in tossing aside attention to phenotype: the would-be constructive breeder must have a rather definite phenotype as his objective; but he should realize that attainment of that goal may, under certain conditions, be somewhat indirect; it may be achieved through the crossing of types neither of which in itself conforms to the objective.

Chromosomes the Mechanism for Segregation. The genes are carried in the chromosomes; or, in other words, the genes are a part of the chromosomes. The chromosomes, therefore, provide not only the mechanism whereby characteristics of the parent are transmitted to the offspring, but they provide also the mechanism whereby segregation takes place in the hybrid.

Figure 22 illustrates the process of maturation, by which, in the production of germ cells, the somatic number of chromosomes is reduced to half, and by fertilization the somatic number is restored. The resulting zygote, therefore, possesses the same number of chromosomes as each of its parents, half of which have been obtained from each parent.

A significant fact in the process of maturation, which should not be lost sight of, is that not *any half* of the chromosome number passes to each daughter cell; each chromosome has its mate, and before reduction the members of each pair of chromosomes draw together, then separate, and one of each pair passes to each of the resulting cells. Thus, each germ cell comes to pos-

sess not *any half* of the parental chromosomes but one of each pair.

Mendel gave no indication of realizing that the factors of inheritance are resident in the chromosomes. The discoveries that the genes (the factors of inheritance) are resident in the chromosomes, that most chromosomes carry many genes, and that the chromosomes possess considerable stability (all facts of heredity discovered since Mendel's time) place limitations on the complete acceptance of Mendel's second law, the law of independent assortment. This point will be discussed in more detail later but it is introduced at this point to aid the student in visualizing the genes and chromosomes.

The Allelomorphic Series. An allelomorph is one of a pair of contrasted factors: for example, P and p form an allelomorphic pair. A gamete can never contain more than one allelomorph, and a zygote, because of its duplicate condition, can never contain more than two allelomorphs. A breed or species may, however, embrace several variations which, taken collectively, constitute an allelomorphic series. Because many such series are known in laboratory animals and plants, there is reason to believe that a similar situation prevails generally in farm animals. For purposes of illustration let it be assumed that the following constitutes an allelomorphic series in cattle and that dominance follows the order of listing: A , A_1 , A_2 , A_3 , A_4 , A_5 , and A_6 . This gives a series of seven allelomorphs, but only one of the seven can be present in any one germ cell and only two can be present in any one zygote. The possible zygotic combinations therefore are:

AA , AA_1 , AA_2 , AA_3 , AA_4 , AA_5 , AA_6
 A_1A_1 , A_1A_2 , A_1A_3 , A_1A_4 , A_1A_5 , A_1A_6
 A_2A_2 , A_2A_3 , A_2A_4 , A_2A_5 , A_2A_6
 A_3A_3 , A_3A_4 , A_3A_5 , A_3A_6
 A_4A_4 , A_4A_5 , A_4A_6
 A_5A_5 , A_5A_6
 A_6A_6

Because of the assumed dominance of the lower numbered A 's there are presented above only 7 phenotypes but 28 genotypes. In only rare instances can the gene members of an allelomorphic series be expected to be equally well represented numerically in

any breed or species. All this has much significance in the modern breeding of farm animals to be discussed later in the book.

The Law of Independent Assortment. This law is known as the second Mendelian law. It is illustrated when individuals possessing two or more contrasting characters are mated. Under the section on the law of segregation (page 103) it was pointed out that in cattle black color is dominant to red and that the polled condition is dominant to horned. Therefore, when a homozygous polled black individual is mated to a homozygous horned red individual, the F_1 will be polled and black. The F_2 generation will, in general, be of four kinds in the ratio of 9 polled black to 3 polled red to 3 horned black to 1 horned red.

Black and polled, therefore, entered the zygote together but did not necessarily come out together, because the genes responsible for color and horns are located on different chromosome pairs. Figure 38 illustrates how independent assortment operates in this case. Owing to chance, the F_1 zygote is as likely to produce germ cells containing chromosomes 1 and 2 as 1 and 2^1 ; or, again, there is as much chance of chromosome 1^1 entering the same germ cell with chromosome 2 as with chromosome 2^1 . Owing to chance, and to large numbers, four types of germ cells are produced. In fertilization chance is again involved; each male gamete is as likely to mate with a female gamete of one type as of another. Thus with large numbers the F_2 population will be of four phenotypes in a 9 to 3 to 3 to 1 ratio. One of each phenotype will breed true: it will produce germ cells of only one kind. The one that will breed true is the one that is homozygous, for example, $PPBB$. The $PpBB$ individual will breed true for black color, but it will produce two kinds of germ cells (for presence or absence of horns), one poll-producing and the other horn-producing. The $PpBb$ individuals will, like their parents, produce germ cells of four kinds. The other individuals of the F_2 generation will produce also germ cells according to their own genetic constitution; those that are homozygous for either character can produce only that kind of germ cell, whereas those that are heterozygous will produce two kinds in equal numbers.

The law of independent assortment may, therefore, be stated thus: two or more pairs of allelomorphic genes may segregate

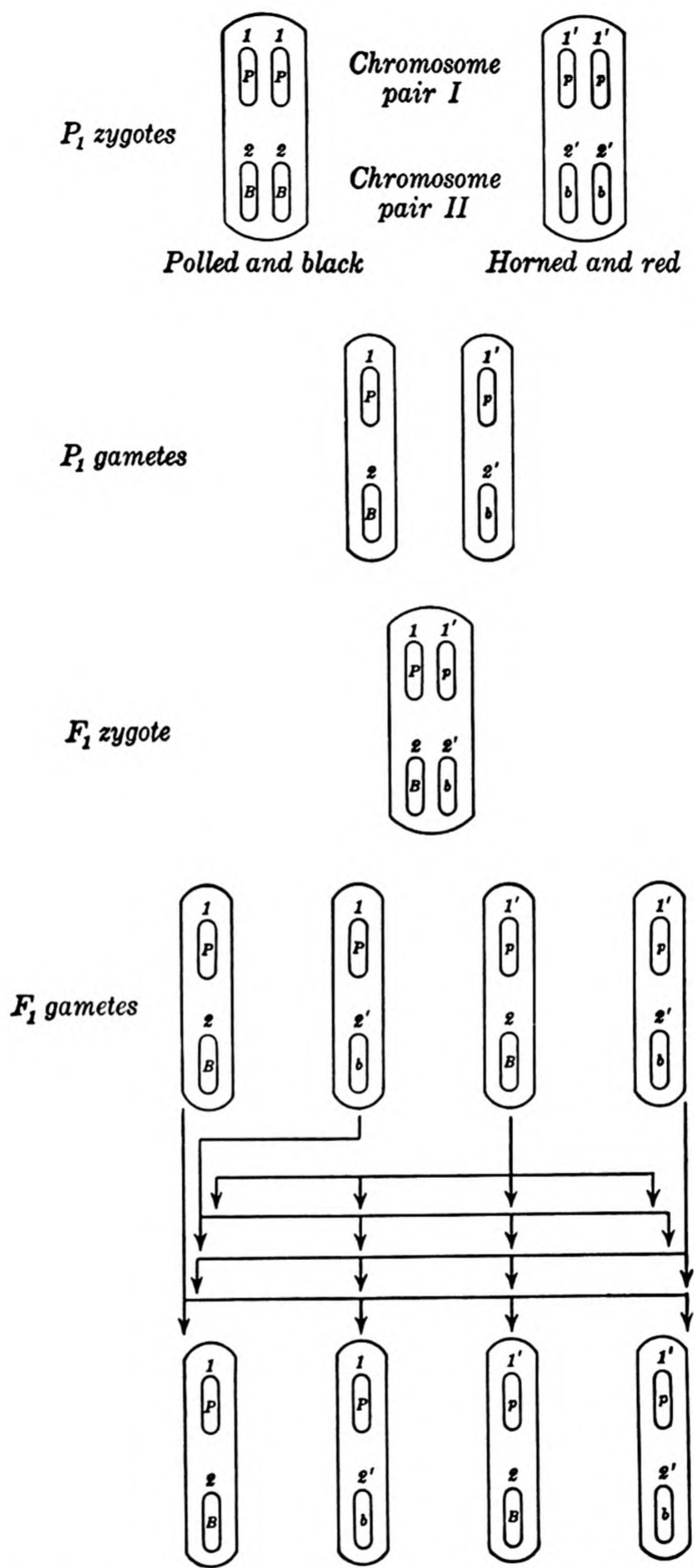


FIG. 38. Illustrating the law of independent assortment of the genes.
(See text.)

independently in the germ plasm of the hybrid and be combined in the subsequent generations in all possible combinations, the number of these combinations being governed only by chance.

When taken advantage of through the crossing of contrasted types, independent assortment offers opportunity for the production of new types in subsequent generations. Most of our present breeds have been produced by the application of this genetic principle; yet until very recently this was accomplished unwittingly. In plant breeding this principle has been applied to advantage during recent years. It appears that constructive animal breeding is likely to follow a similar trend in the near future. This point is discussed more fully later.

Calculating Expectant F_2 Ratios. The calculation of expectant F_2 ratios is not in itself of great importance in practical animal breeding, but it is important, however, in gaining the proper perspective of the problem as a whole. In practical animal breeding the actual calculation of F_2 ratios is seldom encountered, but the ability to think in terms of expectant F_2 and F_3 ratios is highly important to the would-be constructive breeder.

In discussing the calculation of Mendelian expectations Castle (1924) points out that, "The essential point about which one must first of all be entirely clear in his own mind is this—what kind of gametes will each parent form?" To be clear on this point, one must keep in mind a picture of the process of maturation, the process by which one and only one of each chromosome pair finds its way into each germ cell. Germ cells carrying each member of a pair are produced in equal numbers; but chance alone determines whether chromosome 1 or chromosome 1¹ of pair I will enter the same germ cell as chromosome 2 or chromosome 2¹ from pair II, and so on, for all the chromosome pairs (Fig. 38). Therefore, the more numerous the contrasted pairs of characters represented in the zygote, the more numerous are the kinds of germ cells or combinations of factors in the germ cells that the hybrid is capable of producing. In general every additional character in which the individual is heterozygous doubles the possible assortment of gametes which it may produce. (This doubling occurs only if the factors determining these characters are located on different chromosome pairs. Chromosome cross-

OVA

		<i>PBW</i>	<i>PbW</i>	<i>PBw</i>	<i>Pbw</i>
Sperms	<i>PBW</i>	<i>PPBBWW</i>	<i>PPBbWW</i>	<i>PPBBWw</i>	<i>PPBbWw</i>
	<i>PbW</i>	<i>PPBbWW</i>	<i>PPbbWW</i>	<i>PPBbWw</i>	<i>PPbbWw</i>
	<i>PBw</i>	<i>PPBBWw</i>	<i>PPBbWw</i>	<i>PPBBww</i>	<i>PPBbww</i>
	<i>Pbw</i>	<i>PPBbWw</i>	<i>PPbbWw</i>	<i>PPBbww</i>	<i>PPbbww</i>
	<i>pBW</i>	<i>PpBBWW</i>	<i>PpBbWW</i>	<i>PpBBWw</i>	<i>PpBbWw</i>
	<i>pbW</i>	<i>PpBbWW</i>	<i>PpbbWW</i>	<i>PpBbWw</i>	<i>PpbbWw</i>
	<i>pBw</i>	<i>PpBBWw</i>	<i>PpBbWw</i>	<i>PpBBww</i>	<i>PpBbww</i>
	<i>pbw</i>	<i>PpBbWw</i>	<i>PpbbWw</i>	<i>PpBbww</i>	<i>Ppbbww</i> *
		<i>pBW</i>	<i>pbW</i>	<i>pBw</i>	<i>pbw</i>
Sperms	<i>PBW</i>	<i>PpBBWW</i>	<i>PpBbWW</i>	<i>PpBBWw</i>	<i>PpBbWw</i>
	<i>PbW</i>	<i>PpBbWW</i>	<i>PpbbWW</i>	<i>PpBbWw</i>	<i>PpbbWw</i>
	<i>PBw</i>	<i>PpBBWw</i>	<i>PpBbWw</i>	<i>PpBBww</i>	<i>PpBbww</i>
	<i>Pbw</i>	<i>PpBbWw</i>	<i>PpbbWw</i>	<i>PpBbww</i>	<i>Ppbbww</i>
	<i>pBW</i>	<i>ppBBWW</i>	<i>ppBbWW</i>	<i>ppBBWw</i>	<i>ppBbWw</i>
	<i>pbW</i>	<i>ppBbWW</i>	<i>ppbbWW</i>	<i>ppBbWw</i>	<i>ppbbWw</i>
	<i>pBw</i>	<i>ppBBWw</i>	<i>ppBbWw</i>	<i>ppBBww</i>	<i>ppBbww</i>
	<i>pbw</i>	<i>ppBbWw</i>	<i>ppbbWw</i>	<i>ppBbww</i>	<i>ppbbww</i>

FIG. 39. Checkerboard illustration of the *F*₂ expectation from a cross involving three pairs of allelomorphic characters—polled, black-bodied, and black-faced Aberdeen-Angus × horned, red-bodied, and white-faced Hereford.

GENOTYPIC RATIO

<i>1PPBBWW</i> <i>2PPBBWw</i> <i>2PPBbWW</i> <i>2PpBBWW</i> <i>4PPBbWw</i> <i>4PpBBWw</i> <i>4PpBbWW</i> <i>8PpBbWw</i>	<i>1PPBBww</i> <i>2PPBbww</i> <i>2PpBBww</i> <i>4PpBbww</i>	<i>1PPbbWW</i> <i>2PPbbWw</i> <i>2PpbbWW</i> <i>4PpbbWw</i>	<i>1ppBBWW</i> <i>2ppBBWw</i> <i>2ppBbWW</i> <i>4ppBbWw</i>
<i>1PPbbww</i> <i>2Ppbbww</i>	<i>1ppBBww</i> <i>2ppBbww</i>	<i>1ppbbWW</i> <i>2ppbbWw</i>	<i>1ppbbww</i>

PHENOTYPIC RATIO

<i>27PBW</i>	<i>9PBw</i>	<i>9PbW</i>	<i>9pBW</i> *
<i>3Pbw</i>	<i>3pBw</i>	<i>3pbW</i>	<i>1pbw</i>

FIG. 40. A trihybrid Mendelian *F*₂ expectation arranged in the genotypic and phenotypic classes.

* In reading these illustrations the reader must keep in mind that they have been cut at the points indicated by a *. The part below the double line (=), in each figure, is a continuation of the upper part.

overs tend to break linkage relationships; thus when crossing-over occurs the genetic ratios resulting from genes on the same chromosomes fall somewhere between the results of complete linkage and complete independent assortment.) The expected constitution of gametes produced by hybrid parents of the indicated genetic constitution is, therefore, as follows:

Parent	Gametes
Pp	Pp
$PpBb$	PB, Pb, pB, pb
$PpBbWw$	$\{ PBW, PBw, PbW, Pbw$
Etc.	$\{ pBW, pBw, pbW, pbw$

In the above illustration, P is again used to denote polled, B to denote black; and a third character, whiteface, W , is introduced; in cattle W is dominant to w , the self-black condition. $PpBbWw$ is the hybrid that would result from the cross of an Aberdeen-Angus and horned Hereford.

The F_2 expectation may then be calculated by the checkerboard method (Fig. 39) or by expansion of the binomial $a + b$. Multiplying this by itself we get $a^2 + 2ab + b^2$, where the coefficients (1, 2, and 1) of the terms a^2 , ab , and b^2 represent the monohybrid ratio 1 to 2 to 1. If dominance is shown the phenotypic ratio is 3 to 1. The 3 to 1 ratio squared gives the dihybrid ratio of 9 to 3 to 3 to 1; and the 3 to 1 ratio cubed gives the trihybrid ratio of 27 to 9 to 9 to 9 to 3 to 3 to 3 to 1. Their arrangement in their genotypic and phenotypic classes is shown in Fig. 40; it is the arrangement obtained when the various individuals indicated in Fig. 39 are gathered together and placed in their respective genotypic and phenotypic classes.

EXTENSIONS OF MENDEL'S LAWS AND ANIMAL BREEDING

Shortly after the rediscovery of Mendel's laws much was expected of these principles in direct application to both plant and animal breeding. The opinion prevailed that both animals and plants could be subdivided into units and that these units were inherited as a whole. Much was heard of unit characters. Studies were organized to determine these units and their inheritance. The results were disappointing because it became clear that many

characters were not inherited in the simple Mendelian fashion. As a result the opinion developed that not all inheritance was Mendelian. With regard to such quantitative characters as size, rate of growth, milk production, and the like, the term blending inheritance came into use, because it was thought that the germ plasms from the two parents flowed together and mingled much as do two streams of water.

It is not strange that this popular belief should have developed, because Weismann's illustration of the continuity of the germ plasm, which was widely taught by biologists, portrayed essentially that sort of procedure; furthermore it had long been common to speak of bloodlines and the intermingling of different bloods. The result was that animal breeders, with some exceptions, came to regard Mendelian inheritance as an interesting phenomenon but as having little real significance in animal breeding. To some extent the same situation prevailed in the plant field, but it was more limited and of shorter duration. A probable explanation for the difference is that, experiments with plants being much less costly, genetic research was pushed forward in the plant field while nothing of importance was done with farm animals.

Further fundamental studies, especially those dealing with the fruit fly, *Drosophila*, have shown that the original work by Mendel was sound but that Mendel's studies had not explained inheritance in all its details. In fact the original studies by Mendel merely laid a foundation for a more thorough understanding of inheritance; all inheritance, when examined critically, is Mendelian.

Linkage. Mendel wrote of factors as being the units of inheritance. Since then, it has become more common to speak of factors as genes and it was learned that genes are located on the chromosomes somewhat like beads on a string.

Since the factors or genes responsible for the transmission of a character are located on the chromosomes, it follows that when two or more such factors are located on the same chromosome, they will, if there is no crossing-over, be passed from parent to hybrid and from hybrid to its descendants as a unit. Such has proved to be true of a large number of factors. In the *Drosophila*, gray body color, *B*, is dominant to black body color, *b*; and long wings, *V*, is dominant to vestigial wings, *v*. If a long-winged

gray-bodied fly is crossed with a vestigial black-bodied fly, the F_1 will all be long-winged and gray, because black and vestigial are located on the same chromosome, and the allelomorphs, long-winged and gray, are located on the homologous chromosome; hence each pair of genes is linked, that is, they enter the F_1 zygote as pairs, and they pass out paired (Fig. 41). The number of linkage groups, therefore, is dependent upon the number of chromosome pairs possessed by the species in question. Such dependence is revealed by intensive studies of *Drosophila*. The *Drosophila melanogaster* has 4 pairs of chromosomes, and it has been demonstrated that in *Drosophila melanogaster* there are 4 linkage groups. This principle has also been verified in other forms; considerable supporting evidence has been accumulated from studies of corn and laboratory animals.

Drosophila have 4 pairs of chromosomes and 4 linkage groups; the horse has 30 chromosome pairs; hence he may be expected to possess 30 linkage groups. Linkage groups are a limiting factor to independent assortment. Independent assortment exists only between genes located on different chromosome pairs. Not long ago it appeared that this would some day prove an aid in the application of genetic principles to livestock breeding. It appeared that, through the genetic analysis of farm animals, it would be possible to identify chromosome markers and that, when as many independent assorting factors were located as there are chromosome pairs in a species, livestock breeders would know much more about the genetic constitution of their animals and be in a position to mate them more intelligently.

The expansion of knowledge of the fundamentals of genetics and experience in the applications of genetics to animal breeding

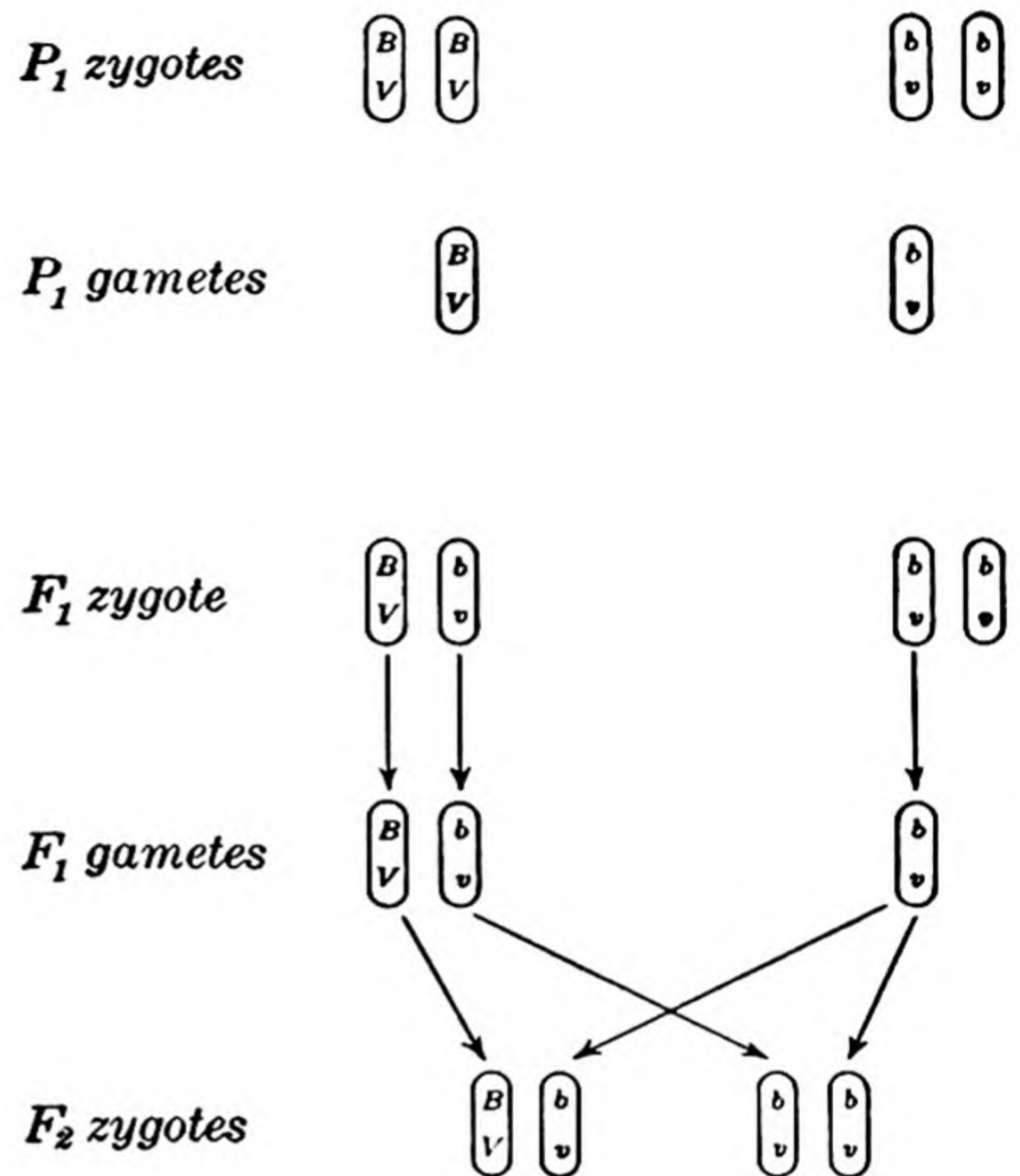


FIG. 41. Illustrating linkage of the factors *B*, gray-bodied with *V*, long wings; and *b*, black-bodied with *v*, vestigial wings. (See text.)

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has made more intelligent mating appear somewhat visionary. It now appears that animal breeders today may expect little from the identification of chromosome markers, but that results similar to those desired may be achieved through other methods of approach. These methods are discussed later.

Crossing-Over. Not all the factors located on the same chromosome show absolute linkage. During the process of maturation and before reduction the members of each chromosome pair come together, twist about each other, and then draw apart (Fig. 19). This process gives an opportunity for an interchange of chromatin material between chromosome pairs. If, then, two factors located on the same chromosome happen to be on either side of the point of crossing-over, they will go in together but will not come out together.

White-eyed miniature-winged female *Drosophila* mated to red-eyed long-winged males will produce F_1 females, all of which have red eyes and long wings. If the F_1 females are back-crossed to a white miniature male, four classes of offspring will appear in the following proportions: 33.5 red long to 16.5 white long to 16.5 red miniature to 33.5 white miniature. Here crossing-over takes place in 33 out of 100 cases. The percentage of crossing-over for the various factors depends, other conditions being equal, upon the distance by which the factors in question are separated from each other on the chromosome.

The chromosomes of farm animals are small in comparison with those of *Drosophila*. Furthermore, there are many more chromosome pairs in farm animals. It may therefore be that linkage is much more nearly absolute in these animals than in *Drosophila*. Nevertheless, crossing-over is a biological fact which must be taken into account in theorizing on the applications of genetics to animal breeding. Crossing-over tends to offset the effects of linkage and thus allows for some assortment of linked genes. Crossing-over makes it possible to develop different linkage combinations in homologous chromosomes. For this reason, even if we had markers on every chromosome, we should have no guarantee of the genetic constitution of our stock. We should merely have an *indication* of their genetic constitution. Under certain conditions such an indication would be extremely helpful. On the other hand, attainment of this end is unlikely until

lines that possess a relatively high degree of homozygosity are developed.

Linear Order of the Genes. Proof of the linear order of the genes is derived directly from linkage data. Crossing-over may occur at many, perhaps any, points on the chromosome. Any two given factors located on the same chromosome show a remarkable consistency in the percentage of crossing-over between them. If, then, the amount of crossing-over between *A* and *B* is 2 per cent and between *A* and *C*, 33 per cent, it is logical to assume that *A* and *C* are located farther apart than *A* and *B*, for the closer the factors the less is the chance of crossing-over. The assumption is that each gene is located on the chromosome in its particular locus, as are different beads on a string. All the members of an allelomorphic series have the same locus on homologous chromosomes; hence only one can be represented in a single chromosome and two in a single zygote.

As a result of much study of crossovers, largely under the leadership of Professor T. H. Morgan, a chromosome map, showing the relative position of the genes of the *Drosophila*, has been drawn (Fig. 42). The distance between genes, however, is not absolute but relative, and it is determined by the percentage of crossing-over.

During recent years the students of corn breeding have made remarkable progress in developing the chromosome map for corn. One school of thought in animal breeding believes that research in animal breeding should be directed along similar lines. Those advocating this approach maintain that the information obtained by other breeding research is largely superficial and that the details of the inheritance of characters and some facts about the chromosome map must be known before breeders will be in a position to deal intelligently with their problems.

Another more recent school of thought declares that, because of the many chromosome pairs and the slow rate of reproduction in farm animals, the students of animal breeding would be working for many decades before they derived much usable information through gene identification. The opinion expressed by this group is that we can accept the fundamental principles of genetics established by students of *Drosophila* and corn genetics, and that the immediate task of the animal breeder is to determine how to apply these principles to animal breeding. They believe

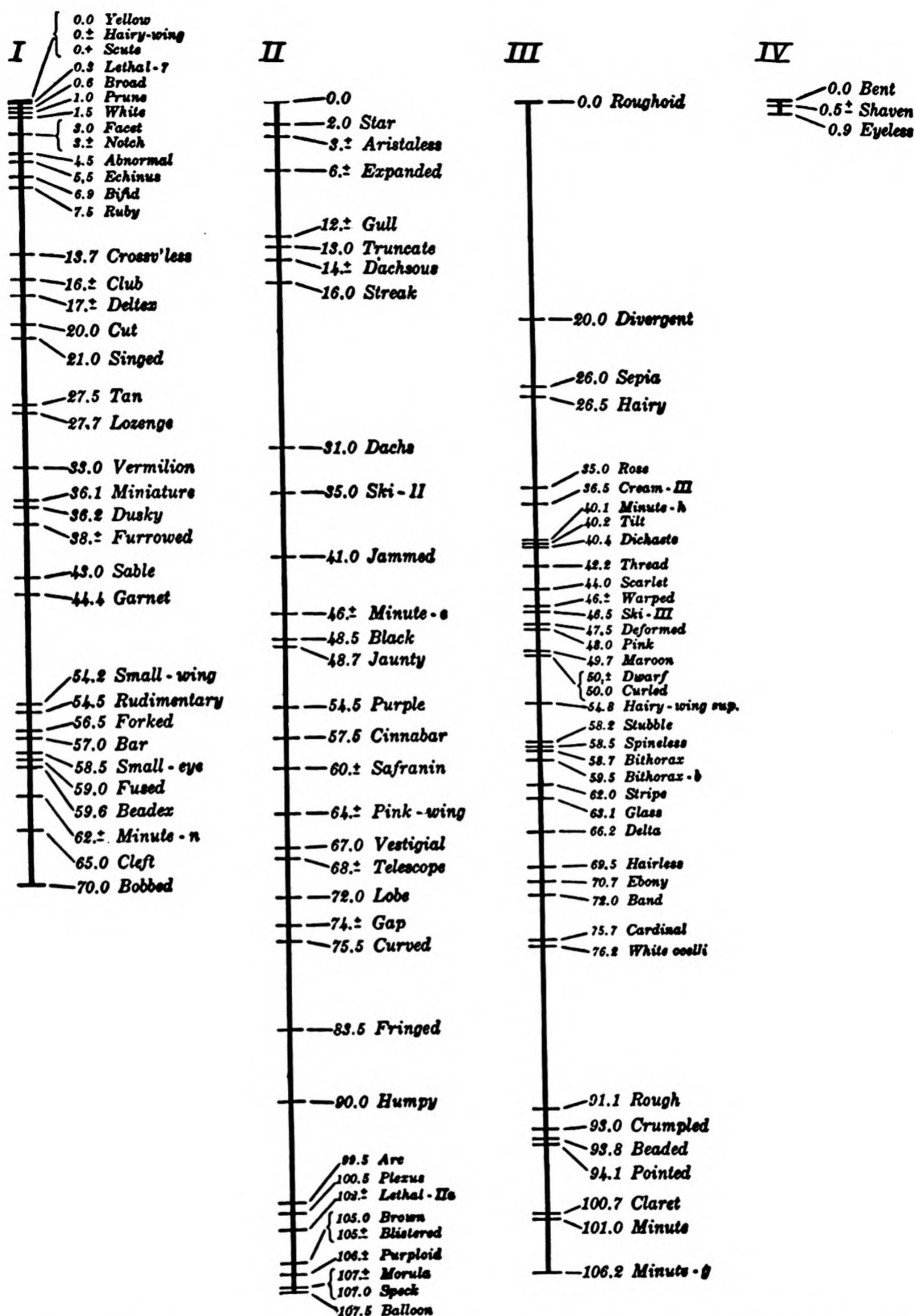


FIG. 42. The chromosome map of *Drosophila melanogaster*. The "map distance" is given in the numerals to the left of each character. (After Morgan, *The Theory of Gene*, Yale University Press.)

that we should already be making greater use of our knowledge of the fundamental principles.

Determining how best to apply the fundamental knowledge of genetics already available is a huge task, and the belief is growing that this should be the immediate job of research workers in animal breeding. Students of animal breeding will do well, however, not to lose sight of the advantage to future animal breeders of gathering as much detailed information as possible on the inheritance of specific characters, such as color and horns. Studies of this type will make possible a gradual approach to chromosome mapping. It now appears clear that gene identification will proceed more rapidly when it is accumulated with studies of systems of breeding (which naturally involve inbreeding and crossbreeding), the immediate problem requiring attention.

Manifold Effects of Genes and the Possibility of Several Genes Affecting the Same Character. It was assumed for some time that a particular character is the product of a single factor, but this is seldom if ever true. The presence and absence of horns in cattle may be due to the interaction of a single pair of genes, but there are many kinds of horns, which may be characterized as Holstein-Friesian, Shorthorn, Hereford, and so on. It is therefore clear that other factors influence the size, shape, color, and texture of the horn produced.

Similarly, it was originally assumed that each gene affects only one character. A single gene may, and usually does, affect many divergent parts of the body; for example, *Drosophila* having rudimentary wings have a lower vitality, most of their females are infertile, and the last pair of legs is often thicker and shorter (Morgan, Sturtevant, Müller, and Bridges, 1923).

Gene Action. The precise chain of events between the gene and the development of the somatic character is unknown. The gene itself is today pictured as a complex organic molecule and as occupying a definite place in a group of such molecules which are arranged in linear order. Gene action is, therefore, visualized for the most part as a long-drawn-out series of chemical reactions. Each gene, therefore, carries a specific chemical load which causes a specific effect or effects, but each gene, or most genes, enter into a chemical reaction with other genes. Most, perhaps all, of these are in turn affected by environment; each chain of

reactions is probably initiated, modified, and terminated by some or several environmental factors. This relationship may be likened to the striking of a match to initiate a fire which in turn is affected and even terminated by draft, moisture, oxygen supply, etc.

It is recognized that the results of gene action may be cumulative (additive) or due to gene interaction. It may be that some genes have only additive effects and other genes interact with others to accomplish the end results; it appears more likely that most genes accomplish their ends both by additive effects and through interaction with other genes. It may well be that additive effects and gene interaction are merely convenient man-made methods of classifying gene action.

Additive Gene Effects. Nilsson-Ehle (1909) in a study of color in crosses of wheat furnished the first definite proof of additive gene effects. For a time this was known as the result of multiple factors. Two varieties of wheat, one red and the other white, when crossed produced F_1 seeds which were red, but the shade was only half as deep as that of the red parent. In the F_2 generation both parental types were recovered, but only about one in sixty-four was white; the F_2 population, taken as a whole, ranged from white to dark red with most of the individuals of the intermediate grades. The interpretation was that red wheat carried three pairs of factors for red, that they were cumulative in their effect, and that dominance was lacking. The genetic constitution of the red wheat may therefore be given as $RR R^1R^1 R^2R^2$, and that of the white wheat as $rr r^1r^1 r^2r^2$. The genetic constitution of the F_1 individuals then is $Rr R^1r^1 R^2r^2$; and the F_2 population consists of every possible combination from $rr r^1r^1 r^2r^2$ and the $Rr r^1r^1 r^2r^2$ to $RR R^1R^1 R^2R^2$ and $RR R^1R^1 R^2r^2$ and $RR R^1R^1 R^2R^2$.

If parental types are to be recovered from crosses involving several multiple factors, the F_2 population must be large, as illustrated in Table VII.

In instances of additive gene effects, the more factors affecting a given character expression that become gathered within a given gene complex, the greater is that character expression. This fact offers an opportunity to improve the character in question through selection. It also presents some limits to effective selection. Let it be assumed that a given character is affected favor-

TABLE VII. THEORETICAL FACTORIAL COMPOSITION OF A POPULATION PRODUCED BY A CROSS INVOLVING MORE THAN A SINGLE MENDELIAN FACTOR, DOMINANCE BEING WANTING

(From Castle, *Genetics and Eugenics*, Harvard University Press)

Factors	Frequencies of F_2 Classes												Total (= $4n$)	Number of Homo- zygotes (= $2n$)	Per Cent of Homo- zygotes
1					1	2	1						4	2	50.0
2				1	4	6	4	1					16	4	25.0
3			1	6	15	20	15	6	1				64	8	12.5
4		1	8	28	56	70	56	28	8	1			256	16	6.2
5		1	10	45	120	210	252	210	120	45	10	1	1,024	32	3.1
6	1	12	66	220	495	792	924	792	495	220	66	12	4,096	64	1.5

ably by the eight multiple factors A , A^1 , A^2 , A^3 , A^4 , A^5 , A^6 , and A^7 . Let it also be assumed that a given strain or line within a certain breed possesses A , A^1 , A^3 , and A^5 and that the individuals within the line possess these factors in varying degrees of purity. This strain may be improved by selection up to the point at which all the individuals have the genetic constitution $AAA^1A^1A^3A^3A^5A^5$. To improve the strain further it will be necessary to cross it to another strain, preferably one that carries the factors A^2 , A^4 , A^6 , and A^7 . Subsequently selection may be effective in increasing the character expression up to the point at which all the individuals in the line are homozygous for the eight factors.

The exact genetic interpretation of multiple factors is extremely difficult and generally impossible in the relatively small populations with which the animal breeder is forced to work. In general, multiple factors call for the use of biometric methods. For this purpose exact measurements are made of the characters of each individual involved in the study. Some characters, such as dimensions and weight, lend themselves readily to measurement. Qualitative characters are often measured with difficulty; in such instances it becomes necessary to develop first special technics by which the character can be measured. After the technic is developed the character in question is converted from a qualitative character to a quantitative one.

Gene Interaction. Few if any genes produce their effects alone. Genes may interact with their allelomorphs or with non-allelic genes. Factor interaction is, therefore, subject to wide divergence in expression. The more specific types of expression are discussed in the following.

Broadened Understanding of Dominance. In Mendel's original discourse, gene expression was described as "all or nothing," dominant or recessive, but it was soon learned that dominance frequently was lacking, and at times incomplete. More recently overdominance has been recognized.

The lack of dominance is illustrated in the inheritance of roan color in Shorthorn cattle. For the most part red \times red matings produce only red calves and white \times white produce only white calves. Red \times white produce roan calves and roan \times roan produce reds, roans, and whites in an approximate 1:2:1 ratio. There are rather wide deviations in all of the above, but they are ascribed both to error in herdbook classifications and to modifying factors, described later in the chapter. The essential point here is that the roan color is the result of the action of a pair of genes (joint action) neither of which is dominant.

Roan color has long been a popular color in Shorthorns; some attempts have been made to develop herds pure for roan. The above makes it clear why those attempts have been futile.

The Palomino horse falls in the above-mentioned category. Palomino color in horses, according to Castle and King (1951), is due to a heterozygous state of the dilution gene, Dd , when combined with bb genes for bay color. It is therefore the combined effect of bb for bay in the homozygous state with the heterozygous state of Dd for dilution that produces the Palomino color.

Partial Dominance. Although Mendel assumed that dominance is complete and although it is now known that dominance may be lacking, in the majority of cases dominance is neither complete nor absent but incomplete or partial and expressed in a variety of ways. In fact, all degrees of dominance exist. Furthermore, dominance is affected by various external and internal influences. It is now known that other genetic factors affect dominance. In the European house mouse the short-tailed mutation generally behaves as a dominant, but when introduced in the Asiatic house mouse it behaves as a recessive.

In the light of present genetic information it may be stated that dominance is not the result of single-factor pairs but that the degree of dominance depends on the animal's whole genetic constitution and on the conditions surrounding its development.

Single-factor identification, therefore, does not carry applied animal breeding very far. The generalizations from the above and other fundamental facts are, however, of major importance in applied animal breeding. Knowledge of these fundamentals gives the breeder a much better conception of his problem and makes it possible for him to develop a stronger breeding program.

Overdominance. This is a condition in which the heterozygous state, Aa , produces a greater over-all effect than either of the homozygous forms, AA or aa . The basic interpretation is that the genes represented by Aa , respectively, enter into some sort of interaction or yield additive effects whereby a greater net result is produced by the heterozygous state than by either homozygous one. This can be visualized as being brought about by any one of several different basic gene actions.

Let it be assumed that the Aa condition results in greater growth than either the AA or aa condition. If A and a each produce as much or nearly as much growth alone as in the homozygous state and A and a differ in timing action, then the Aa condition should result in more growth than either of the homozygous states.

On the other hand, it is well known that most animals encounter varied environmental conditions during their growth. If then A responds more favorably to one type of environment and a to a different environment, it is easy to visualize the Aa condition as producing more favorable results than AA or aa . This may be why the more highly heterozygous individuals generally pass through unfavorable environmental conditions more successfully than the more nearly homozygous, even though under favorable environments the more nearly homozygous may equal or nearly equal the heterozygotes in performance.

If genes are accepted as being complex organic molecules, then it is easy to visualize a chemical interaction between A and a that is different and greater than the reaction of either AA or aa .

Overdominance is of importance in hybrid vigor, and its significance is discussed in greater detail in that portion of the

book (see page 246). The author is inclined to believe that lack of dominance, incomplete dominance, and overdominance are all varied expressions of dominance and not markedly different from one another except in over-all effect.

The Epistatic Condition. An *epistatic* factor is one which prevents a factor other than its allelomorph from exhibiting its normal effect on the development of the individual. The factor that is prevented from exhibiting its normal effect in the development of the individual due to an epistatic factor is known as *hypostatic*. This condition is frequently confused with dominance especially in attempts to make interpretations from the F_1 . In reality it is similar to dominance except that it occurs between different factors, whereas dominance occurs between two members of an allelic pair.

Ibsen (1933) points out that the B of the Angus is epistatic to the Bs of the Jersey. When the BB Angus is crossed with the BBs Jersey the offspring are black like the Angus. The interactions of B and Bs and their allelomorphs as given by Ibsen follow:

BB	$BsBs$, black
BB	$bsbs$, black
bb	$BsBs$, black and red
bb	$bsbs$, red

The cross of the Angus and Jersey is further complicated because the Angus carries the factor Br . The joint action of Br and Bs is necessary to produce brindle color. When the Angus and Jersey are crossed and the offspring mated *inter se* the results are indicated below:

Parental generation: BB $bsbs$ $BrBr$ \times bb $BsBs$ $brbr$					
(Angus, black)			(Jersey, black and red)		
F_1 :	Bb	$Bsbs$	$Brbr$	(black)	
F_2 :	27	B	Bs	Br	
	9	B	Bs	br	
	9	B	bs	Br	
	3	B	bs	br ,	48 blacks
<hr/>					
	9	b	Bs	Br ,	brindles
	3	b	Bs	br ,	black and reds (Jerseys)
	3	b	bs	Br	
	1	b	bs	br ,	4 reds (Guernseys)
<hr/>					

For the F_2 only the zygotes are represented. The homozygous and heterozygous dominants are represented by only one letter. The recessives are also represented by only one letter.

Another illustration of epistasis is found in the inheritance of white color in poultry. The white plumage of the White Wyandotte and White Plymouth Rock is recessive to the self-colored condition. The white of the White Leghorn, however, is almost completely dominant to the self-colored condition of other birds. The interpretation is that the recessive white birds are white because they lack the basic color factor, and that the White Leghorn carries the basic factor for color, but remains white because of the presence of some other factor that acts as an inhibitor. This interpretation is made because, when White Leghorns are crossed with White Wyandottes or White Dorking, the F_1 are white with colored flecks, and in the F_2 both white and colored individuals appear in a 13:3 ratio.

If I indicates the inhibitor and C the colored factor, the genetic constitution of the White Leghorn is $IICC$ and that of the recessive parent, $iicc$. The F_1 birds are $IiCc$, white with colored ticks. The F_2 birds present the usual dihybrid genotypic ratio:

$IICC$	$Iicc$	$iiCC$	$iicc$
$2IICc$	$2Iicc$	$2iiCc$	(white)
$2IiCC$	(white)	(colored)	
$4IiCc$			
<hr/>			
9(white)	3	3	1

In the above ratio any zygote containing I will be white, those containing II will be pure for white, and the $iicc$ individual will be white because color is absent from its genotype.

Thus we observe that the fundamental principles of Mendel's work remain undisturbed, but that the dihybrid phenotypic ratio is very different from the conventional 9:3:3:1 ratio. The breeder of animals through the selection of phenotypes probably will encounter many obstacles. In the foregoing illustration different genetic combinations produce white. They cannot be distinguished from one another by their appearance. As a result the breeder breeding for white on the basis of phenotypic selection will have colored birds produced for many generations to come. Instances of this kind help to account for the generally

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prevalent belief that many generations of breeding and selection are required before a new strain of animals can be justly labeled a breed.

The epistatic condition may well play an important rôle in instances of prepotency. A sire possessing an epistatic pair of factors when mated with females possessing hypostatic genes may appear prepotent.

Modifying Factors. Although it is known that in *Drosophila* eye color is due to a single factor, seven other factors that cause modifying effects have been identified. In mice, white-spotted pattern behaves as a simple recessive to self-colored coat, but spotted mice range from nearly self-colored to nearly all-white. The variations are attributed, for the most part, to modifying factors which affect the white spotting.

The effect of the dilution gene, *D*, on color in horses has already been mentioned (page 120). Its action as a modifier will be discussed here.

The three basic genes for color in wild animals are *A*, *B*, and *C*. *C* is the designation of a dominant gene for the production of melanin pigment in the hair and skin. Its allelomorph *c* in the homozygous condition, *cc*, results in albinism.

B designates a dominant gene which with *C* produces black pigment. Here we have two different genes combining in their action to give a definite end result. The gene *B*'s allelomorph in the homozygous state changes the black to brown, which is a less completely oxidized melanin pigment.

A, mentioned above, is a dominant gene which modifies the expression of *B* and *C* so as to produce *agouti* or wild coat pattern. In the domestic horse it modifies the action of *B* and *C* to produce bay color.

D is used to designate a dilution gene which reduces the intensity of all pigmentation. *D* in the homozygous state, *DD*, combined with *bb* results in what is called a type *A* albino. The *DDbb* genetic state results in what is called a type *B* albino. Neither of the above are, however, true albinos; the true albino condition can result only from the presence of *cc* genes.

The buckskin or dun color is produced by the *Ddbb* genetic state and, as already given, the Palomino from the *Ddbb* state.

The above illustrates the modifying effects that some genes have on the expressions of others. It appears likely that the more

important characters such as fertility, vigor, growth, etc., are affected by many modifiers.

Complementary Factors. Certain factors cannot express themselves except in the presence of some other factor, or the modification of their expression may be due to the presence of some other factor. This is merely another type of expression of gene interaction. It appears that umbilical hernia in swine is at least stimulated by two independently inherited factors. In the author's experiments, two inbred lines, *A* and *B*, were crossed, and females with umbilical hernia were produced in every litter. No case of umbilical hernia had been recorded in the ancestry of either line during their development as an inbred line. Line *A* was then crossed with line *C*, which also had a record of no umbilical hernias, and again the umbilical hernia was produced in the cross. The F_1 from both crosses were culled for the umbilical hernias and inbred, and in both instances the hernias disappeared from the lines in two generations. The conclusion was that line *A* was carrying a factor potent for hernia which expressed itself when introduced in the genetic environments provided by *B* and *C*. Crosses between *B* and *C* did not develop hernias.

White Silkie fowl mated to White Dorking produce F_1 which are all colored. The F_1 mated *inter se* produce a ratio of 9 colored to 7 white. In this particular case, each of the white birds evidently carried one of the factors necessary for color. If the factors for color are indicated by *A* and *B* as used by Crew (1925), the constitution of the P_1 individuals may be described by *AAbb* and *aaBB*. Their offspring will be *AaBb*, and they will be colored because both *A* and *B* are necessary for the production of color. The F_2 genetic ratio will be the usual dihybrid ratio, but the F_2 will exhibit a 9 to 7 phenotypic ratio because both *A* and *B* are necessary for the production of color. The genotypes and phenotypes of the F_2 are:

<i>AABB</i>	<i>AAbb</i>	<i>aaBB</i>	<i>aabb</i>
2 <i>AABb</i>	2 <i>Aabb</i>	2 <i>aaBb</i>	
2 <i>AaBB</i>			
4 <i>AaBb</i>			
<hr/>			
9 colored		7 white	

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Coat color in rodents yields an F_2 ratio of 9:3:4. When black mice are crossed with albinos the F_1 are agouti, the wild type of color. When the F_1 are interbred the progeny on the average yields a ratio of 9 agouti to 3 black and 4 white. The genotypes and phenotypes of the F_2 are:

$CCAA$	$CCaa$	$ccAA$	$ccaa$
$2CCAa$	$2Ccaa$	$2ccAa$	
$2CcAA$			
$4CcAa$			
<hr/>			
9 agouti	3 black	4 white	

In this case the agouti or wild type is brought out by the joint action of A and C . The C factor is necessary for the production of black, but black is changed to agouti when C is in the presence of A . The white individuals are white because the gene for color is absent.

It may also be assumed that the wild agouti color was lost during domestication because of the separation of the genes A and C , and that many other important characters have been altered during the process of domestication and breed formation by similar procedures. If characters can be markedly altered by changes in the gene associations, at least one of the major tasks of the constructive animal breeder is to alter the gene associations to obtain more and more favorable results, and then to fix those combinations so that they can be reproduced practically at will.

Another good illustration of complementary factors is Walnut comb in fowl. Single, Rose, Pea, and Walnut are all fowl comb patterns. In experimental breeding, both Rose and Pea proved dominant to Single, and the natural assumption was that the three formed an allelomorphic series, but when Rose was mated to Pea, Walnut resulted. When the Walnuts were mated *inter se*, Walnut, Pea, Rose, and Single were obtained.

The genetic interpretation is that two factors are concerned, R and P . The Singlecomb pattern is single because neither R nor P is present; therefore, Rosecomb \times Singlecomb produces Rosecomb, and Peacomb \times Singlecomb produces Peacomb. But the presence of both R and P is necessary for the production of Walnutcomb. The hypothesis is that all fowl possess the factors for Singlecomb and that R and P modify the single factor, but

the factor S for Singlecomb may be disregarded because all fowl are supposed to possess it in the duplex condition.

The genetic constitution of the various phenotypes may therefore be represented as

$RRPP$	$RRpp$	$rrPP$	$rrpp$
$2RRPp$	$2Rrpp$	$2rrPp$	
$2RrPP$			
$4RrPp$			
<hr/>			
9 Walnut (RP)	3 Rose (Rp)	3 Pea (rP)	1 Single (rp)

In this illustration it is possible by inbreeding and selection to obtain a homozygous or true breeding Walnut, because R and P are apparently located on different chromosome pairs. But if R and p (and in like manner r and P) had been located on the same chromosome (not allowing for crossovers) it would have been impossible to obtain a homozygous strain of Walnuts.

It probably makes no difference whether a strain is purified for Walnut. Characters of economic importance are, however, just as likely to be affected by complementary factors. Furthermore, there is no reason to believe that factor interaction is confined to two pairs of factors; there is reason to believe that usually many pairs are involved. If the characters are of a quantitative nature, the expression is less clearly marked than in the above instance.

The complementary action of factors is merely another expression of gene interaction. It appears that the various expressions of dominance and gene interaction are very similar basically, but that they differ in their expressions.

Fundamental Genetics and Animal Breeding. At this point the student of animal breeding will do well to take time for reflection and meditation. Segregation, independent assortment, allelomorphic series, linkage, crossovers, dominance, and gene interaction offer much food for thought with reference to possibilities for recombinations and explanations for the many variations that continue to plague the breeder. The breeder's job is both to appreciate these possibilities and to learn how to capitalize on them.

CHAPTER IX

Lethals

The term lethal is generally applied to a genetic factor that causes death of the organism in which it occurs, death occurring either during prenatal life or at birth. A broader definition of a lethal is that it is a factor which, because of certain defects which it produces, leads eventually to death of the organism. Factors which eventually cause death are frequently designated as semi-lethals or sub-lethals. The definition is frequently

P_1 zygotes, yellow	Yy	Yy	
P_1 gametes	Y	y	
	Y	y	
	<hr/>		
	$1YY,$	$2Yy,$	$1yy$
F_1 zygotes	(pure yellow)	(yellow)	(non-yellow)
	(dies)		

FIG. 43. Illustrating the inheritance of a lethal factor in mice.

broadened to include such undesirable characters as hernia and cryptorchidisms. Characters of the latter type do not necessarily destroy the individuals, but they interfere with their usefulness.

One of the first lethals discovered was in a certain yellow variety of the house mouse. It was observed that this variety never breeds true. When mated *inter se* the progeny are 1 gray, brown, or black to 2 yellow. If the yellows are mated to non-yellows, a 2 non-yellow to 2 yellow ratio results. This is what is to be expected from mating a heterozygote to a recessive homozygote. The interpretation is that yellow, Y , is dominant to non-yellow, y ; and that the Y gene is lethal when in the homozygous condition (Fig. 43).

Many of the defects now known to be due to lethal factors have long been recognized in farm animals; they were previously described as monstrosities, freaks, and the like. The search for lethals in farm animals has not been especially intensive. In fact it has been mostly a by-product in the field of animal breed-

ing; yet so many lethals have been noted that it appears that lethals may not have received the attention they should have in both practical and scientific considerations of animal improvement.

Typical Illustrations of Lethals. *Achondroplasia*₁. *Achondroplasia*₁ is the condition that has long been known as the bull-dog calf. The legs are very short. The head is thick and short. The nose is flattened, the upper lip split, the lower jaw protruding, and the tongue swollen and protruding.

Bull-dog calves are usually aborted between the third and the eighth months. Delivery when close to term is usually difficult because of the extremely large head.

This type of calf is reported to have occurred in the Dexter breed and in African cattle. About one-fourth of the calves born from Dexter × Dexter matings are bull-dogs. These same matings produce what is known as the Kerry-type cattle, a type having longer legs and narrower heads than the Dexters. It appears that the Dexter type is produced when the animal is heterozygous for this particular dominant gene. The gene in question causes short legs and the correct type of head. Matings *inter se* bring about segregation; one-fourth are homozygous for the gene and are bull-dogs; one-half are heterozygous and are Dexter type; one-fourth are homozygous for absence of the gene and are Kerry type.

*Achondroplasia*₂. This is another bull-dog type but it is less extreme than the above. It is reported to have occurred in the Telemark and the Holstein breeds, and the author has observed it in the Guernsey breed. These calves are usually carried to term. As a rule they are unable to stand, and they die within a few days of birth.

The character has been described as recessive; hence it appears only in animals that are homozygous for this recessive gene.

Epitheliogenesis Imperfecta. Calves with this condition have skin defects on the lower legs and hairless patches on the body. The mucous membranes of the mouth and the nostrils are defective. The ears and the claws are often deformed. The calves are usually born at term but die as a result of bacterial invasion. The condition is due to a simple recessive. Calves with this defect are reported to have appeared in the Holstein and the Jersey breeds and in the cattle of Holland. The author has observed Shorthorn calves of the same type.

A condition known as congenital ichthyosis is probably closely allied to the above defect. It is due to a simple recessive. The skin is scaly and cracked.

Foetal Resorption. Stages varying from decomposed masses to only bones or dried mummies have been reported. It is likely



FIG. 44. A cow egg that was fertilized but when recovered, 3 days 16 hours after the passing of heat, showed indications of disintegration, and the egg was not so far advanced in segmentation as it should have been for its age.

that many embryos die while still in the ovum or embryo stage (Fig. 44). The modes of inheritance of lethals of this type have not been determined. Until the inheritance of an abnormality is established, it is well to withhold judgment on its being an inherited lethal because faulty nutrition and environment are also frequently lethal.

Muscle Contracture in Swine. Pigs with this defect are born with stiff forelegs. The pigs are dead at birth or die shortly after. This is probably the same character as *thick forelimbs*, caused by

a gelatinous infiltration of the connective tissue near the bones. It appears to be due to a simple recessive.

Muscle Contractures in Sheep. Affected lambs have stiff joints and a crooked neck. They are usually stillborn. A similar condition has been reported in cattle. The condition is due to a recessive.

Congenital Loco in Poultry. Chicks with this condition are unable to stand when hatched. The head is drawn back with the beak pointing upward, usually to one side. Later the chick loses its balance and falls on its back or side. About 88 per cent die within a month. It behaves as a simple recessive.

Creeper in Poultry. Birds of this type are characterized by very short legs and wings, both somewhat deformed; they are heterozygous for the creeper gene. The homozygous individuals usually die during the fourth day of incubation; they possess limbs so shortened that the feet appear attached directly to the body.

This character has been said to be due to a dominant gene. Actually the gene is only partially dominant, as the heterozygous individuals possess less of the character than the homozygous individuals possess, and they survive.

Thought regarding lethals as with most topics has undergone a series of changed views as to their significance and mode of in-

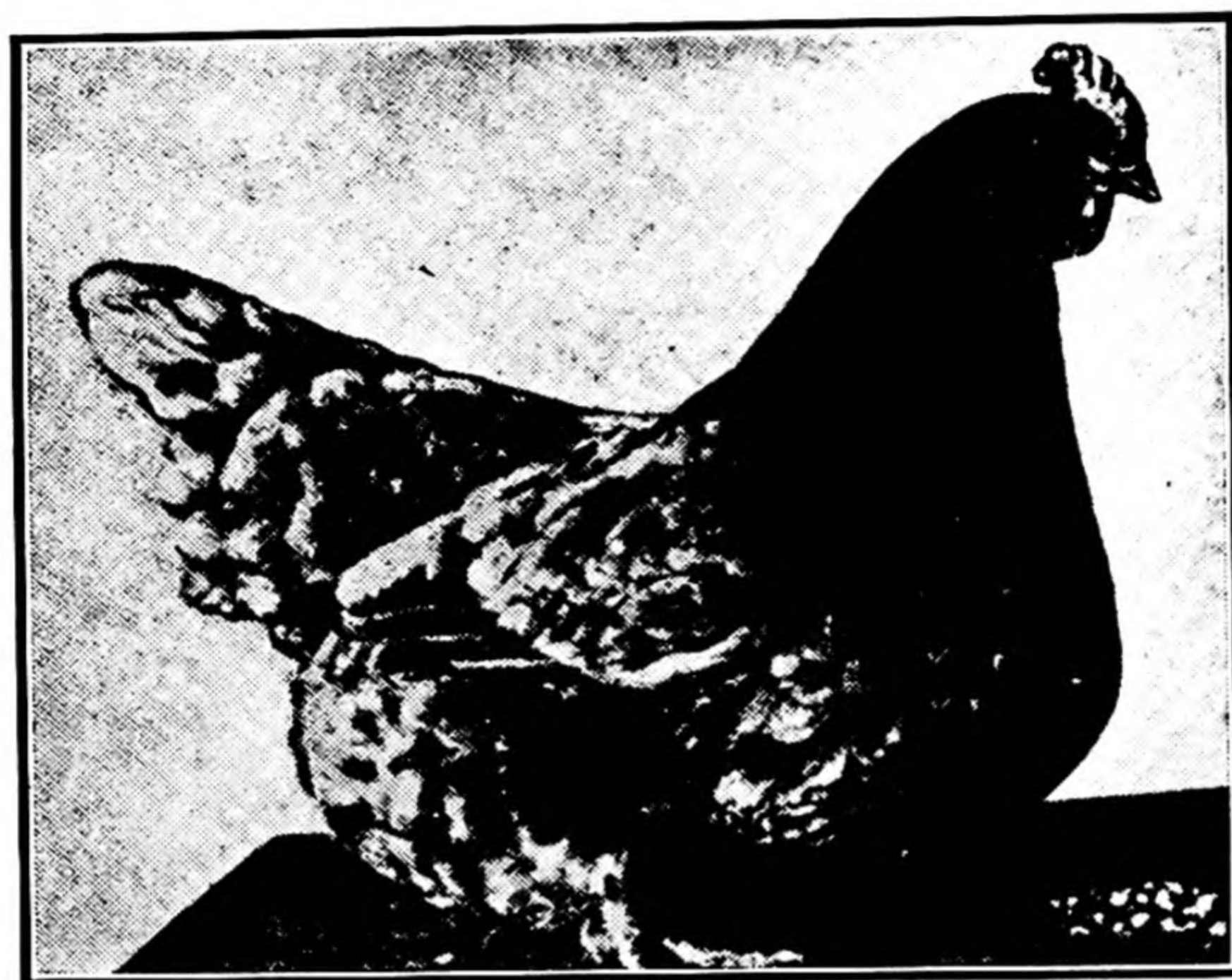


FIG. 45. A creeper; a bird that is heterozygous for the creeper gene. (After Cutler, from Hutt, in *Cornell Veterinarian*.)

heritance. The tendency at first appears to have been oversimplification. More data and modification may clarify some of the present vagueness regarding their modes of inheritance.

Lerner (1944) did an excellent job of cataloguing and bringing our information on lethals among farm animals up to that date. The following is from his paper in the *Journal of Heredity*:

A. CATTLE

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
A1	<i>Achondroplasia</i>	Endocrine defect affecting skeleton. Heterozygotes exhibit <i>achondroplasia</i> .	Seligmann, 1904 JPB 9:311. Wilson, 1909 RDS 12:1. Crew, 1923 RS 95:228. Crew, 1924 RSM 17:39. Punnett, 1936 JG 32:65.
A2	<i>Epitheliogenesis imperfecta</i>	Denudation of skin facilitating bacterial invasion, which leads to <i>septicaemia</i> .	Cole, 1919 JH 10:303. Hadley and Cole, 1923 WRB 86. Hadley, 1927 JH 18:487. Hadley and Warwick, 1927. JAVMA 70:492. Regan, Mead, and Gregory, 1935 JH 26:357. Wipprecht and Horlacher, 1935 JH 26:363.

A. CATTLE (*Continued*)

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
A3	<i>Achondroplasia</i>	Milder form than exhibited in dominant <i>achondroplasia</i> ; affected calves born alive. The cases described by Gregory <i>et al.</i> are phenotypically distinct from the others.	Wriedt, 1925 ZTZ 3:223. Mohr, 1926 ZiAV 41:59. Weinkopf, 1927 BTW 43:62. Wriedt, 1930 HL. Carmichael, 1933 N 131:878. Punnett, 1936 JG 32:65. Brandt, 1941 JH 32:183. Gregory, Mead, and Regan, 1942 JH 33:317.
A4	<i>Hypotrichosis congenita</i>	Hairlessness; affected calves die shortly after birth.	Mohr and Wriedt, 1928 JG 19: 315. Wriedt, 1930 HL. Butz, 1934 DTW 42:653. Eisele, 1936 Z 11:432. Johansson, 1941 IGCE :169.
A5	<i>Acroteriasis congenita</i>	Appendages partly absent—"amputated"; jaws deformed; affected calves often stillborn.	Wriedt and Mohr, 1928 JG. 20:187. Wriedt, 1930 HL.
A6	Mummification	Stiffened legs, shortened neck, many fetuses mummified at term.	Loje, 1930 TL 10:517.
A7	Lameness	Affected calves born alive, but lame in hind legs.	Loje, 1930 TL 10:517.
A8	Muscle contracture	Head, neck, and limb muscles affected; affected calves may be born alive.	Mohr, 1930 NV 14:1. Hutt, 1934 JH 25:41.
A9	Ankylosis of jaw	Articulation of lower jaw ossified.	Mohr, 1930 NV 14:1.
A10	Short spine	Fusion of vertebrae resulting in shortened spine; affected calves stillborn or die at birth.	Mohr and Wriedt, 1930 JG 22:279.
A11	Ljutikow's lethal	Inferred from records of still-born calves. Contrary to description in other check-lists, Ljutikow finds no recorded evidence of abnormalities in the still-borns.	Ljutikow, 1932 BZ 1:21.
A12	Congenital dropsy	Accumulation of water in body cavity and subcutaneously; affected calves born alive.	Larsson, 1935 LVH :310. Johansson, 1941 IGCE :169.
A13	General ankylosis	All joints ossified; cleft palate.	Stang, 1940 ZZ 46:280.
A14	Impacted molars	Premolars impacted; "parrot-mouth" appearance; affected calves alive at full term.	Heizer and Hervey, 1937 JH 28:123.
A15	Achondroplastic micromelia	Calves cannot survive on pasture because of imperfection of lower jaw in addition to shortened limbs.	Ljutikow, 1937 BZ 6:413.

A. CATTLE (*Continued*)

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
A16	<i>Atresia ani</i>	Imperforate anus; affected calves do not survive surgical treatment.	Kuppuswami, 1937 IJ 7:305.
A17	Deformed limbs	Crooked legs, sometimes with ankylosis. Calves stillborn or, if alive, unable to stand.	Ruzhevsky, 1938 BZ 7:547.
A18	Brain hernia	Opening in skull involving frontal and parietal bones; affected calves either born alive or stillborn.	Shaw, 1938 JH 29:319.
A19	<i>Agnathia</i>	Lower jaw half the length of normal; affected calves unable to nurse.	Annett, 1939 JG 37:301.
A20	<i>Agnathia</i>	Jawless, accompanied by wattlelike structure. All cases studied were foetal.	Ely, Hull, and Morrison, 1939 JH 30:105.
A21	Sex-linked lethal	Evidence of existence based on abnormal sex ratios (shortage of males).	Andreesen, 1940 ABA 10:24.
A22	Abnormal skull	Nasal openings fused. Die at birth or shortly after. Possible inhibitor of lethal expression also found.	Ilancic, 1940 Z 15:129.
A23	Missing phalanges	First and second phalangeal bones missing; otherwise calves born at full term are normal.	Johansson, 1941 IGCE :169.
A24	Hydrocephalus	Internal hydrocephalus accompanied by bone abnormalities.	Cole and Moore, 1942 JAR 65:483.
A25	Congenital spasm	Vertical intermittent spasms of head and neck. Calves die shortly after birth.	Gregory, Mead, and Regan, 1944 JH 35:195.

B. HORSES

B1	<i>Atresia coli</i>	Closure of colon, often associated with brain defects; colts born alive.	Nusshag, 1925 BTW 41:646. Yamane, 1925 FEATM :815. Yamane, 1927 ZiAV 46:188.
B2	Fredriksborg lethal	Evidence for existence inferential; high degree of sterility in inbred matings of white horses led to the postulation of existence of a lethal factor.	Wriedt, 1924 ZTZ 1:231; 1930 HL.
B3	Sex-linked lethal	Evidence of existence based on abnormal sex ratios (shortage of males).	Kislovsky, 1932 ZTZ 24:269.
B4	<i>Epitheliogenesis imperfecta</i>	Denuded skin on limbs, occasionally missing hoof. Born alive but none of 5 observed colts survived. Evidence of hereditary nature of defect inferential.	Plank, 1936 NFTA :233.

B. HORSES (*Continued*)

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
B5	Deformed forelimbs	Atrophied muscles or lack of balance between tendons.	Prawochenski, 1936 JH 27:411.
B6	Umbilical hernia	No information given by author.	Prawochenski, 1941 IGCE :241.
B7	Absence of eyes, orbits	No information given by author.	Prawochenski, 1941 IGCE :241.

C. SWINE

C1	Brain hernia	Skull opening involving frontal and parietal bones; affected piglings born alive.	Goldsmith, 1922 JH 13:69. Nordby, 1929 JH 20:229. Hughes and Hart, 1934 JH 25:111.
C2	Paralysis	Hind limbs paralyzed; affected piglings born alive.	Mohr, 1930 NV 14:1.
C3	<i>Atresia ani</i>	Closure or <i>diverticulum</i> of anal opening in piglings born alive; mode of inheritance not clear.	Kinzelbach, 1931 ZiAV 60:84. Carstens, Wenzler, and Dürr, 1937 Z 12:205. Berge, 1941 JH 32:271.
C4	Cleft Palate	Affected piglings born alive but unable to nurse; line died out before genetic nature of this condition was definitely established.	McPhee, Russell, and Zeller, 1931 JH 22:393. Koch and Neumüller, 1932 DTW 40:353.
C5	Thickened forelimbs	Muscle fibers displaced by connective tissue infiltration; affected piglings born alive.	Walther, Prüfer, and Carstens, 1932 Zr 7:178. Carstens, Wenzler, and Dürr, 1937 Z 12:205.
C6	Muscle contracture	Rigid forelimbs; affected piglings usually stillborn.	Hallquist, 1933 H 18:219.
C7	Split ears	Associated with deformed hindquarters and sometimes cleft palate; affected piglings usually born dead.	Annett, 1938 JH 29:469.
C8	Hydrocephalus	Fluid found in subarachnoid spaces; affected piglings sometimes stillborn.	Blunn and Hughes, 1938 JH 29:203.
C9	Amputated	Both front and hind appendages completely missing, though shoulder blades and pelvic bones present; affected piglings born alive.	Johnson, 1940 JH 31:239.

D. SHEEP

D1	Muscle contracture	Flexure of limbs and wry neck; affected lambs stillborn.	Roberts, 1926 JMA 33:795. Roberts, 1929 JG 21:57.
D2	Earless and cleft palate	Often associated with tripartite claws; apparently, affected lambs are born alive (listed as "sublethal" by Mohr).	Mohr, 1929 Z 4:105.
D3	Paralysis	Hind limbs paralyzed; affected lambs born alive.	Zophoniasson, 1929 NJ 11:327.

D. SHEEP (*Continued*)

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
D4	Rigid fetlocks	Skeleton, including skull, deformed and associated with short wool and a hernia; affected lambs born alive.	Zophoniasson, 1929 NJ 11:327.
D5	Amputated	Limbs amputated at fetlocks; mode of inheritance not clear.	Kroon and Planck, 1931 TD 58:681. Kroon and Planck, 1932 BG 8:213 Höhn, 1942 DTW 50:349.
D6	Lethal gray	2 gray to 1 black ratio observed in matings between gray parents. No homozygous gray adults found. 3 gray to 1 black observed in matings between gray parents, but no homozygous gray adults found. Presumed homozygotes die in early postnatal life; digestive disturbances associated with cause of death.	Constantinescu, 1932 INZR 1:15. Glembotsky, 1935 PZ (2):41. Contescu and Epureanu, 1939 ZTZ 44:211.
D7	Dwarf	Thyroid disturbance leading to death within a month after birth.	Bogart and Dyer, 1942 JAS 1:87.

E. CHICKENS

E1	Creeper	Shortened extremities in heterozygotes. Homozygotes usually die in first week of incubation.	Cutler, 1925 JH 16:353. Landauer, 1941 SB 236 contains bibliography of numerous papers.
E2	Congenital loco	Affected chicks unable to stand, head bent backwards.	Hamburger, 1942 BS 6:311. Knowlton, 1929 OB :253.
E3	Sticky	Lack of absorption of amniotic and allantoic fluids; bones deficient in calcium; affected embryos die in last week of incubation.	Byerly and Jull, 1932 JEZ 62:489.
E4	Wyandotte lethal	Linked with recessive white in the Wyandotte breed.	Dunn, 1932 AN 57:345.
E5	Congenital palsy	Tremor affecting hatched chicks; occasionally affected chicks survive.	Hutt, 1932 IGC 2:96. Hutt and Child, 1934 JH 25:341.
E6	Cornish lethal	Shortened extremities in heterozygotes. Homozygotes die in last week of incubation.	Landauer, 1935 JG 31:237.
E7	Sex-linked lethal	Evidence of existence based on abnormal sex ratios (shortage of females).	Upp and Waters, 1935 PS 14:372.
E8	<i>Amazilla</i>	Maxillae absent or reduced, beak bent to one side; most of the affected chicks unable to hatch.	Asmundson, 1936 JH 27:401.

E. CHICKENS (*Continued*)

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
E9	Flightless	Defective structure of flight feathers. No homozygotes raised to maturity.	Warren, 1937 JH 28:17.
E10	Malformed skeleton	Curvature of spine and pelvis; birds developing the defect are unable to move. Several recessive genes postulated, but data given inadequate to formulate any definite conclusions.	Czaja, 1939 WPCC :55.
E11	Naked	Affects feather follicles, reducing down and plumage; sex-linked; half of the affected chicks hatch, but only half of these survive.	Hutt and Sturkie, 1938 JH 29:371.
E12	Short beak	Upper mandible and certain long bones shortened; 87% of homozygotes die before hatching.	Landauer, 1941 G 26:426.
E13	<i>Microphthalmia</i>	Diameter of eyeballs reduced; mortality occurs in late embryonic or early post-hatching stages.	Jeffrey, 1941 JH 32:310. Gruenwald, 1944 AR 88:67.
E14	<i>Micromelia</i>	Two genes involved: double recessives exhibit "parrot-beak" and shortened and thickened extremities.	Asmundson, 1942 JH 33:328.
E15	Talpid	Affected embryos exhibit extra digits in fore and hind limbs, frequently webbed; ectopia always present; homozygotes usually die at 8-10 days of incubation.	Cole, 1942 JH 22:83.
E16	Chondrodystrophy	Extreme type of bone modification; affected embryos fail to hatch.	Lamoreux, 1942 JH 33:275.
E17	Deformed mandibles	Lower mandible missing, upper deformed; surviving homozygotes unable to pip shell; cerebral hernia present.	Marble, Harper, and Hammers, 1944 PS 23:114.
E18	Wingless	Wings absent or vestigial, affected embryos do not survive.	Waters and Bywaters, 1943 JH 34:213.
E19	"Chondrodystrophy"	Shortened bones of limbs, but no parrot beak; few homozygotes hatch, none surviving beyond 7 days after hatching.	Hays, 1944 AN 78:54.

F. TURKEYS

NUMBER	CHARACTER	COMMENTS	INVESTIGATORS
F1	Albinism	Sex-linked recessive; only about a quarter of carrier females hatch; most of these do not survive for long, largely because of blindness associated with absence of pigment.	Hutt and Mueller, 1942 JH 33:69.
F2	Short spine	Shortened neck and body; affected embryos fail to hatch.	Asmundson, 1942 SEBM 50:120.

G. DUCKS

G1	Crest	Heterozygotes crested; homozygotes have cerebral hernia and do not hatch.	Rüst, 1932 AG 6:110.
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List of Abbreviations in Literature References

ABA— <i>Anim. Breed Abstr.</i>	JMA— <i>J. Ministry Agr.</i>
AG— <i>Arch. Geflügelk.</i>	JPB— <i>J. Path. Bact.</i>
AN— <i>Am. Naturalist</i>	LVH— <i>Lantbr. Veck. Handl.</i>
AR— <i>Anat. Rec.</i>	N— <i>Nature</i>
BG— <i>Biol. Generalis</i>	NFTA— <i>Nene Forsch. Tierz. Abstammungsl.</i>
BS— <i>Biol. Symposia</i>	NJ— <i>Nord. Jordbrugsf.</i>
BTW— <i>Berlin. Tierärztl. Wochenschr.</i>	NV— <i>Naturens Verden</i>
BZ— <i>Biol. Zhurn.</i>	OB— <i>Ore. Agr. Exp. St. Bull.</i>
CV— <i>Cornell Vet.</i>	PS— <i>Poultry Sci.</i>
DTW— <i>Deutsch. Tierärztl. Wochenschr.</i>	PZ— <i>Probl. Zhivotn.</i>
FEATM— <i>Trans. Sixth Congr. Far East. Assoc. Trop. Med.</i>	RDS— <i>Proc. Roy. Dublin Soc. N. S.</i>
G— <i>Genetics</i>	RS— <i>Proc. Roy. Soc. B.</i>
H— <i>Hereditas</i>	RSM— <i>Proc. Roy. Soc. Med.</i>
HL— <i>Heredity in Livestock</i> , Macmillan, London	SB— <i>Storrs Agr. Exp. St. Bull.</i>
IGCE— <i>Proc. Seventh Int. Genet. Congr. Edinburgh</i>	SEBM— <i>Proc. Soc. Exp. Biol. Med.</i>
IGCI— <i>Proc. Sixth Int. Genet. Congr. Ithaca</i>	TD— <i>Tijdschr. Diergenesek.</i>
IJ— <i>Indian J. Vet. Sci. Anim. Husb.</i>	TL— <i>Tidsskr. Landok.</i>
INZR— <i>Ann. Inst. Nat. Zootech. Roumanie</i>	WPCC— <i>Proc. Seven World's Poultry Congr. Cleveland</i>
JAR— <i>J. Agr. Res.</i>	WRB— <i>Wis. Agr. Exp. St. Res. Bull.</i>
JAVMA— <i>J. Am. Vet. Med. Assoc.</i>	Z— <i>Züchtungsk.</i>
JEZ— <i>J. Exp. Zool.</i>	ZiAV— <i>Zeit. ind. Abst. Vereb.</i>
JG— <i>J. Genet.</i>	Zr— <i>Züchter</i>
JH— <i>J. Hered.</i>	ZTZ— <i>Zeit. Tierz. Züchtungsbiol.</i>
	ZZ— <i>Zeit. Zücht. B.</i>

Dwarfism in Cattle. Since about 1945, dwarf calves of beef cattle breeding have been reported with increased frequency. They have been reported in the literature by Johnson, Harshfield, and McCone (1950); Baker, Blunn, and Oloufa (1950); Baker, Blunn, and Plum (1951); and Gregory *et al.* (1951). Dwarf calves have been reported as appearing in the three major beef breeds. The economic loss is serious; it is not confined only

to the small adult size of the dwarf calves and their inability to grow rapidly, but the condition causes considerable difficulty and losses, especially among heifers, at calving.

The evidence indicates that a single autosomal recessive gene when in the homozygous state is responsible for the condition.



FIG. 46. A 16-month-old calf—a "dwarf." (Courtesy Dr. Carl Roubicek.)

It appears, however, that the gene may differ for different breeds, because a dwarf of one breed mated to a dwarf of another may not produce a dwarf. This could, of course, be due to a change in the genetic environment brought about by the crossing of breeds; that is, the modifying factor complex was so changed as to prevent the expression of dwarfism. The phenotypic appearances of dwarfs as reported are not identical. This, too, could be due to different basic genes for dwarfism or to different sets of gene modifiers.

Dr. P. W. Gregory of the University of California has contributed greatly to the solution of this problem. Dr. Gregory *et al.* (1952) have a special instrument for recording the profile of cattle heads. By this means he is able to recognize, with a very high degree of accuracy, the bulls that are heterozygotes. It has also been shown that normal cattle have different profile types and that these different profile types have some association with the degree or type of dwarfism expressed.

The heterozygotes have a head type that found considerable favor in the show ring. This in turn has led to the selection of herd sires with this type of head. The genes for dwarfism apparently have thereby become so widely dispersed as to be a serious problem to the herds and breeds concerned.

If dwarfism is due to a single autosomal gene, it could be eliminated, provided that breeders were serious in their desire to eliminate the condition. It would, of course, be necessary to eliminate the type associated with the heterozygous genotype. This in itself would not be of any serious consequence to the industry, but it would be to many individual breeders with heavy investments in that type of cattle.

The heavy pressure of selection for small size and ultra refinement may have led to a rather unbalanced genetic state which provided a favorable environment for the full expression of the genes for dwarfism.

The above has some support from the studies of MacArthur (1944). MacArthur developed a large and a small race of mice. From the fifth to the seventh generations a number of what MacArthur calls runts (11 out of 212 males and 15 of 239 females) segregated as recessives from the small line only. Their vitality was low, and apparently they were sterile. Selection against the parents producing them essentially eliminated the type.

MacArthur states: "These basic data clearly suggest that the influence of a size gene or modifier is not a constant quantity definable in absolute amount, but rather that the effect of such a size gene or modifier increases as body size increases and lessens as body size diminishes. In other words, the characteristic and essential effect of a size gene is that it depends on some standard of reference and is relative, being proportional to body size as potentially determined by the remainder of the genotype."

If then we are to interpret the above in terms of dwarfism in cattle, it could mean that selection for ultra refinement had produced a genotype in which the "dwarf" gene was able to express itself more forcefully than in other genetic environments. It would also explain why small-type matings do not always produce the expected percentage of dwarfs; in some cases the dwarf gene may not be present.

Lethals and Animal Breeding. Not all the characters labeled as caused by hereditary lethals have been proved to be inherited. Nevertheless, a sufficient number of hereditary lethals have been identified to cause stockmen concern. It appears likely that many hereditary lethals are still uncovered. It is not known how disadvantageous it may be to an animal to be heterozygous for a recessive lethal. Sub-lethals are probably far more serious than lethals because they are more likely to be carried along unnoticed; yet they may be causing considerable damage.

A condition due to the presence of sub-lethals and one due to an undesirable gene complex may be so similar that it is difficult to recognize where one leaves off and the other begins. In practice it probably makes little difference because the constructive breeder's job is to eliminate both.

A further possible complicating factor may be gene interaction. It is now well recognized that a given gene may be dominant in one gene complex and recessive in another. It is therefore logical to assume that the action of genes in producing lethals may, in some instances at least, not be comparable. If that assumption is true it further complicates exact identification of the gene or genes responsible, but it does not alter the basic problem, the elimination of this genetic material from the family or breed in question.

An inbreeding program designed to purge a stock of lethals and sub-lethals should prove beneficial to any breed. The bad results frequently accompanying inbreeding are in part due to the uncovering of lethals and sub-lethals. Inbreeding is the most certain and quickest means of bringing lethals to light and giving the breeder the opportunity of culling them.

In cases where a given lethal is widely dispersed through a major segment of the livestock population and threatens serious damage, it does not appear practical to attempt the immediate complete eradication of the lethal from the entire population.

A cheaper and, perhaps in the end, more effective method of at first reducing the incidence of the phenotypic expression of the lethal, and later practically eliminating it, would appear to be through the development of herds certified as free of the lethal in question. This could be accomplished through a combination of progeny testing, particularly of sires, and some inbreeding. A sire in question could be certified as free of the defect (in case the defect was due to a single gene in homozygous condition) if he had been mated to twelve females, known to be heterozygous for the defect, and none of the offspring exhibited the defect. The proof, of course, would not be absolute, but it would be so highly improbable that the male in question was heterozygous for the lethal gene that it would be practical to certify him as free of the defect. By developing this sort of nucleus and then breeding the stock from within, in order to prevent the introduction of the lethal gene, such a foundation or foundations could eventually be used to furnish sires for a larger segment of the livestock industry, and eventually the presence of the recessive gene, though not completely eliminated, could be reduced in frequency so as to cause negligible damage.

Where the heterozygous types of bulls can be identified with a high degree of accuracy, as in dwarfism, the direct elimination of the heterozygotes on the basis of phenotype is the proper procedure.

CHAPTER X

Sex

Sex determination and sex control have long been of great interest to both the layman and the biologist. The ancients advanced theories of the cause of sex determination. The number of theories advanced increased through the ages. Many of these still enjoy a wide following. The beginning of a sound understanding of sex determination came through the rediscovery of Mendel's laws and the discovery of the accessory chromosome.

The Accessory Chromosome. Dr. C. E. McClung, an eminent American zoologist, first suggested that the odd (uneven numbered) chromosome found in

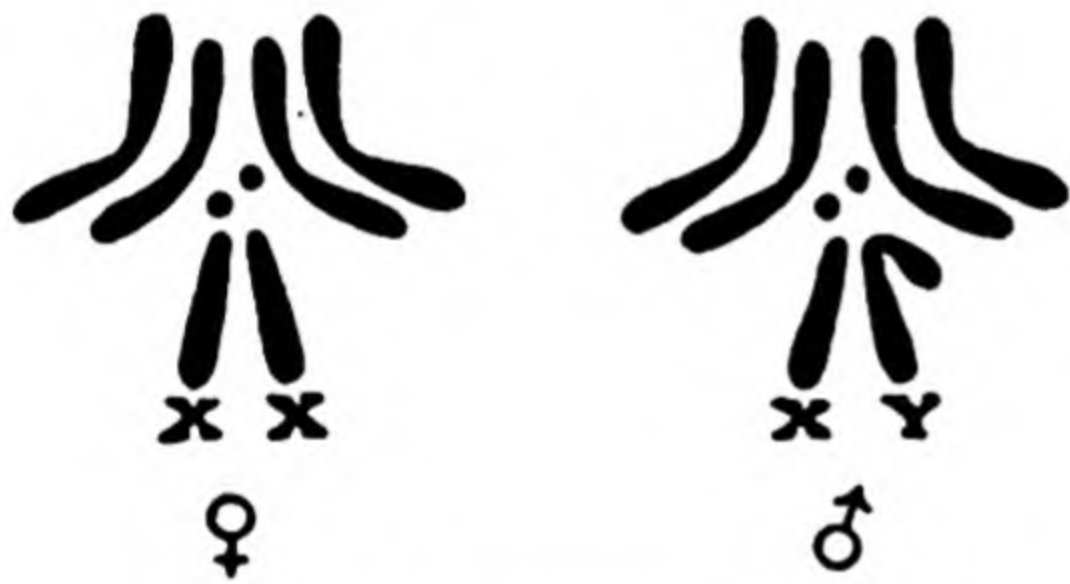


FIG. 47. Conventional diagram of the chromosomes of *Drosophila melanogaster*. (After Morgan.)

many insects might be a determiner of sex. Dr. E. B. Wilson, another eminent American zoologist, first proved that McClung's suggestion was correct. Wilson showed that the male squash bug produces two kinds of sperm, one containing 11 chromosomes and the other, 10. He also showed that the matured egg contains

11 chromosomes; that, if it is fertilized by a sperm having 10 chromosomes, a male zygote having 21 chromosomes results; and that, if the egg is fertilized by a sperm carrying 11 chromosomes, a female zygote carrying 22 chromosomes results.

Morgan discovered sex-linked inheritance in *Drosophila* which led him to assume that the female *Drosophila* possessed two X-chromosomes, which were both sex-determiners and the carriers of sex-linked genes, and that the male possessed only one X-chromosome. Later it was discovered that the male *Drosophila* possessed a mate to the X-chromosome that was distinguishable from the X because it commonly had a hook on one end. This chromosome was called the Y-chromosome.

The somatic cell of the *Drosophila* contains 8 chromosomes; by the process of reduction, during maturation, they are reduced to 4, which in the female consist of two large, curved autosomes (chromosomes other than sex), one small autosome, and one club-shaped chromosome called the *X*-chromosome—a sex-determiner. The male matures two kinds of germ cells: one like that of the female, and the other different only in that the sex chromosome, in place of being club-shaped, has a hook; this is called the *Y*-chromosome—male-determiner. Since the somatic

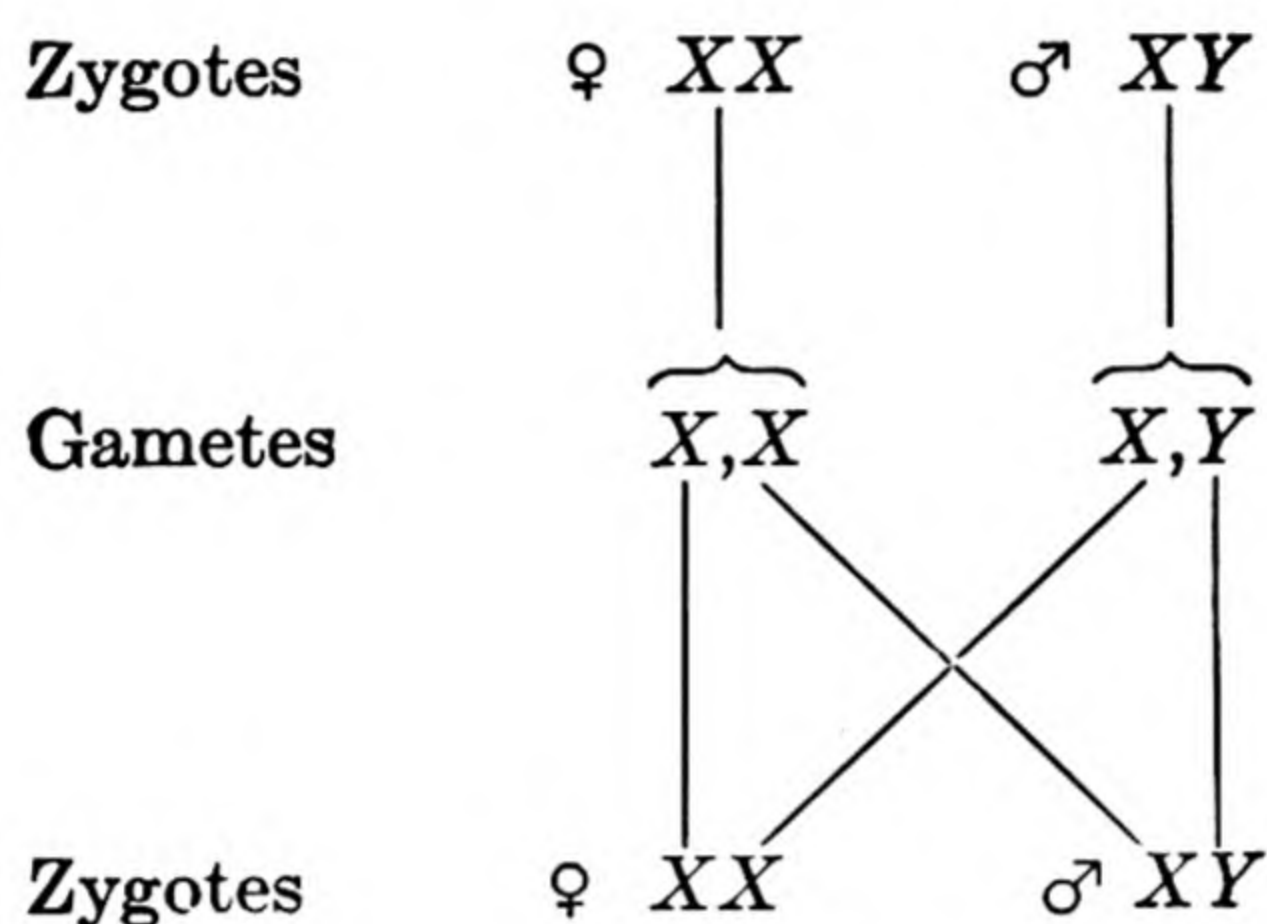


FIG. 48. Illustrating sex determination by the *X* and *Y* mechanism.

cell contains 1 *X*- and 1 *Y*-chromosome, these male and female determining germ cells are produced in equal numbers; hence sex determinations depend on the random mating of the germ cells.

It has been accepted that the *XX-XY* type of sex determination holds true for mammals; that is, the female is homozygotic regarding sex and therefore produces only one kind of sex gamete, whereas the male is heterozygotic regarding sex and therefore produces two kinds of sex gametes, and these are in equal numbers. In certain instances there may be a slight aberration from the above; the *Y*-chromosome may be empty or missing.

In birds and moths the situation is reversed. The male is homozygous and produces gametes of only one kind, whereas the female is heterozygous and produces two kinds. This is generally known as the *ZW* type, the male being *ZZ* and the female *ZW*. Castle (1924) suggests that the *X-Y* terminology be maintained and then proceeds to label these males as *YY* and the females *XY*. By so doing he maintains consistency in ascribing female determination value to the *X*-chromosome. His termi-

nology if used generally would avoid considerable confusion among students.

Castle also suggests that the X-chromosome of birds is probably not homologous to the X of mammals. It is his opinion that birds and mammals evolved independently from an antecedent hermaphroditic state.

The X- and Y-Chromosome Not the Full Explanation of Sex Determination. If the above explanation were the full explanation of sex determination, there would be no place for the intersexes or the sex reversals which are known to occur. Nor would we have a sound basis for the known facts regarding the embryonic differentiation of sex: up to a certain stage of embryonic development the two sexes are equally well developed. As aptly put by Lillie (1939) (in Allen's *Sex and Internal Secretions*), "Every zygote is thus potentially hermaphroditic in the sense that it is capable of giving rise to characters of either sex, or, subject to conditions of determiners, to characters of both sexes, i.e., to individuals that are actual gynandromorphs or intersexes. . . . In the development of every individual, therefore, there occurs, at some time at least, the rudiments of all sex characters, whether male or female."

In insects and amphibia complete sex reversal, the production of a functional male from a genetically determined female, or vice versa, has been produced by experimental procedure. It has been closely approximated in birds. In mammals sex differentiation has not been brought under such complete control, but significant changes in sex differentiation have been observed.

The Autosomes and Sex Determination. In *Drosophila melanogaster*, by a certain back-cross, Bridges (1939) (in Allen's *Sex and Internal Secretions*) obtained normal females and individuals which were apparent intersexes. The latter could be divided into two classes, male intersexes and female intersexes. Both groups of intersexes were sterile. Cytological examinations showed them to possess the following chromosome complex:

		Male Intersex	Female Intersex
Chromosome	II	3	3
"	III	3	3
"	IV	2	3
"	X	2	2
"	Y	Present in some	Present in some

Somatic division does not always follow the orderly process of mitosis. Bridges has described examples of ordinary diploid females with ovaries having certain areas in which the component cells are much larger than normal, the chromosomes of which are tetraploid. A tetraploid female will produce $2N$ gametes (gametes with double the normal number of chromosomes). A diploid ovum fertilized by a normal gamete will give rise to a $3N$ zygote. The assumption is that such a mother gave rise to the intersexes mentioned above.

The chromosome difference between the intersexes and females is that the former possess an extra set of autosomes. The discovery of this fact has made it clear that the autosomes are concerned with sex determination and that their action is male-determining. This does not preclude the possibility of there being female-determining genes on the autosomes; it does indicate, however, that the male determiners are more powerful in their total effect, either through greater numbers or through potency.

The X -chromosome, on the other hand, throws development toward the female side, as shown by the fact that an extra X in a male group changes the male into a female. Individuals that possess $2X$ and $2A$ (two X -chromosomes and two sets of autosomes) are normal females; thus an X outweighs the effects of one set of A 's. Bridges represents the net effectiveness of the X for female tendency as 100 and the net effectiveness for maleness of a set of autosomes as 80. In an individual possessing $2X$ to $2A$ (normal female) the ratio of female effectiveness to male effectiveness is 200 to 160 or 1.25 to 1. Thus 1.25, which Bridges

TABLE VIII. RELATION OF SEX TO CHROMOSOMES IN *Drosophila melanogaster*

(From Bridges in Allen's *Sex and Internal Secretions*)

Sex Type	X(100)	A(80)	Sex Index	Interval, Per Cent
Superfemale	3	2	1.88	50
Female	4 N	4	1.25	50
	3 N	3	1.25	50
	2 N	2	1.25	50
	N	1	1.25	50
Intersex	2	3	0.83	33
Male	1	2	0.63	50
Supermale	1	3	0.42	

calls a sex index, is the index of a normal female. The sex index remains the same for females which possess 1, 2, 3, or 4 sets of chromosomes (Table VIII). The normal male is X to $2A$, and has a normal sex index of 0.63. The sex index for the superfemale is 1.88, which is derived from a $3X$ to $2A$ chromosome complex. The supermale possesses X to $3A$ and a sex index of 0.42. The intersexes are indicated by possession of $2X$ to $3A$ and a sex index of 0.83. Bridges' scheme of sex indexes is presented in Table VIII.

Metabolism and Sex Determination. It has been shown by Riddle (1923) that males possess a higher rate of oxidation and females a lower rate. He also has evidence that the difference in rate of oxidation is a determining factor in sex differentiation. The result, however, is the same; it merely means that a zygote of the XY type establishes a higher rate of oxidation than one of the XX types. Riddle's and Bridges' explanations are both useful in helping to explain more of the details of normal and abnormal sex development. Both explanations are in keeping with the most modern, ever-growing concept of genetics, that most characters result from the interaction of several genes and that the genes achieve their results through a series of physiological reactions.

The unit-character concept of gene action was discarded many years ago, but it left in its wake an aftereffect that was somewhat out of harmony with the above.

The Hormones and Sex Differentiation. Hormones may or may not play a part in primary sex determination. They do, however, play a part in sex differentiation and sex reversals. A classic in this field is Lillie's (1917) explanation of the freemartin. It had long been known that a female calf born as a co-twin to a male calf is usually sterile and possesses some of the sex characters of both sexes. It is known as a freemartin. Lillie found that fusion of the chorions and vascular anastomosis occur in the bovine when the twins are between 10 and 15 millimeters in length. There is a free exchange of blood between the two shortly after the 15-millimeter stage of development.

The above facts gave rise to Lillie's hormone theory of the freemartin which, in brief, is that the male calf casts hormones in its blood, and that these flow to the female calf and stimulate the recessive characters present in the female embryo, thus caus-

ing the sterile freemartin. In all the examples of two-sexed twins examined by Lillie, where vascular anastomosis had taken place, the female was a freemartin; and where vascular anastomosis had not taken place, the female was sexually normal. He also found male twins and female twins, in which vascular anastomosis had taken place; they were all perfectly normal. The evidence, therefore, strongly indicates that the freemartin is fundamentally a female but is changed by the exchange of blood with the male.

Lamb twins are also found in a single chorion, and the question naturally arises: "Why do we not have lamb freemartins?" But, in these instances, vascular anastomosis does not take place.

Another question that arises naturally is: "Why is the female twin always affected?" The answer is that there is evidence that the male's genital organs develop at an earlier age than the female's organs; therefore the male hormones stimulate the latent male characters in the female before the female characters are stimulated by her own hormones. Whitehead (1904) has considerable data on pigs, reviewed by Lillie (1917); they show that in the male the genital organs develop earlier than in the female. According to Whitehead's work, interstitial cells are present in both the testis and the ovary of the pig at the 2.5-centimeter stage, but, whereas they are very numerous in the testis at this stage, they are very rare in the ovary. If it is assumed that a similar condition prevails in the bovine foetus, the hormone theory is a very plausible explanation for the occurrence of the freemartin.

Other Cases of Intersexuality in the Mammal. Crew describes goats, pigs, horses, bovines, sheep, and camels which early in life were apparently normal females, but which later assumed some of the male characteristics. Examination of the internal genitalia of intersexed pigs revealed that the individuals possessed some of the genitalia of both sexes. They could be divided into two classes: those in which the gonads were entirely composed of testicular tissue and those in which in greater or less degree both ovarian and testicular tissue existed. Among the latter, there were instances in which the gonads consisted of: one ovary and one testis; one ovary, the other an ovotestis; both ovotestes; and in one case paired ovaries and paired testes.

The above cases are not to be explained as further examples of the freemartin because their mode of development is known to be different.

The explanation offered rests upon the known facts that at a certain stage of embryonic development the individual possesses (1) a pair of indifferent gonads, which develop later into female or male gonads; and (2) Müllerian and Wolffian ducts which develop into female or male genital tracts, respectively, depending upon whether the gonads develop into ovaries or testes. Presumably the development is due to hormones secreted by the respective gonads; whether the gonads become male or female depends upon the gene complex of the individual. The theoretical explanation offered is that the different male-determining and female-determining gene complexes elaborate their sex-differentiation substances at different rates or come into action at different times. Abnormality in the time or rate of the elaboration of the above would then account for the intersexed individuals.

Sex Ratio and Its Control. In normal cases sex determination is dependent upon the chance mating of the gametes; hence one would expect the sex ratios to be equal, but they are not necessarily. Crew (1925) gave the following sex ratios:

	Male	Female		Male	Female
Man	103-107	100	Pig	111.8	100
Horse	98.3	100	Rabbit	104.6	100
Dog	118.5	100	Mice	100-118	100
Cattle	107.3	100	Fowl	93.4-94.7	100
Sheep	97.7	100	Pigeon	115	100

By inbreeding and selection King (1918 and 1919) developed one strain of albino rats with a sex ratio of 122 males to 100 females, and another strain with a sex ratio of 82 males to 100 females.

Some evidence indicates that the sex ratio varies with the season of the year.

Sex ratios as tabulated at birth are secondary sex ratios; hence they may differ from the primary sex ratio. If, for any reason, one sex is weaker than the other during the early stages of development that sex will suffer a high mortality, and the sex ratio will be altered accordingly. Sex-linked lethals give cause for some upsets in the expected sex ratio.

Since sex is determined by the random choice of the gametes, if any environmental influence weakens one kind of gamete more than the other, the sex ratio may be altered. Various proposals have been advanced for control of the sex ratio by destroying or handicapping one type of gamete (male- or female-determining). The latest of these was proposed by Prof. Felix Unterberger of Prussia. In the United States considerable publicity was given to Unterberger's methods by the *New York Daily News* and by Carl Warren (1940). The proposed method of sex control was to use a 1.5 to 2.0 per cent soda douche previous to mating when male offspring were desired and a 0.5 to 1.0 per cent lactic acid douche if female offspring were wanted. The strength of the solutions was varied somewhat for different species.

Drs. McPhee and Eaton (1942) of the United States Department of Agriculture made a thorough test of the recommended methods: 2,322 rabbits and 121 pigs were born in their experiments. The results were distinctly negative. Similar experiments, but conducted on a smaller scale, were carried out at Illinois, Texas, and Wisconsin; the results likewise were negative.

CHAPTER XI

Selection

Selection consists of choosing the parents of the next generation. Degrees of selection vary, and the term itself has different meanings to different people. Many arguments about selection are really more concerned with the methods employed than with the word "selection."

Selection in animal breeding concerns itself with differential rates of reproduction. Those animals in a flock or herd that produce more offspring will have a greater chance to have their young selected. In most herds or flocks, some animals are marketed before they have had a chance to reproduce; others are kept to produce offspring. Unless the market animals and the ones saved for breeding are separated entirely at random, some selection is being practiced. It is doubtful if any breeder ever saves his breeding stock entirely by chance. He is more likely to keep animals on the basis of personal preference. He hopes these animals will produce more animals like themselves.

Allowing some animals to produce no young and others to produce all of the next generation is only one illustration of how selection is really a matter of choosing parents of future generations. There are many degrees of this practice. For example, in a swine herd where two boars are used on an equal number of females, the boars should have equal opportunity to leave offspring for the next generation, other things being equal. If the breeder, however, saves 75 per cent of his replacement gilts from sire *A*, and only 25 per cent from sire *B*, then *A* has three times the opportunity to contribute to future generations that *B* has. Selection is being practiced for the offspring of *A*, even though both sires leave some offspring in the herd.

The Reason for Selection. Selection is carried on for a variety of traits. In race horses selection is for more speed. In dairy cattle selection is directed to higher milk and butterfat

production. In pet stock and often in farm stock also, selection is for appearance. In farm animals, selection should always be directed to greater utility.

One central idea serves as a guide to all selection, regardless of what trait or class of animal is being subjected to selection, namely, a belief that selection will be effective in producing the results for which the breeder is striving. This holds true, even though the degree to which people believe selection to be effective varies widely.

Why do we believe that selection will be effective? There is evidence from at least three sources. The first line of evidence comes from the study of evolution. In studying the line of descent of the horse, for example, it has been shown that the early ancestors were very different in size and in many other characters from the present-day horse. It has further been shown that natural selection has been the effective agent in shaping the changes in the horse and in all other organisms.

This was known to Charles Darwin in the nineteenth century. Darwin, however, did not know that natural selection worked through definite hereditary units called genes. Since Mendel's discovery of the laws of inheritance, this knowledge has gradually been supplied by students of genetics and evolution. This has given rise to a fairly sound understanding of how evolution has worked. It can now be clearly stated that selection on the basis of small genetic differences, and an accumulation of these small differences, has brought about major changes in our plants and animals. Evolution thus shows that selection is effective over long periods of time, and indicates that we shall be successful in improving farm animals if we can duplicate and speed up the process of evolution.

The second line of evidence shows that animal breeders have, in fact, succeeded in speeding up and directing the work of evolution. They have evolved breeds in all classes of livestock. They have been successful in increasing the yield of wool in sheep, the quantity and quality of meat in meat animals, and the quantity of milk and butterfat in dairy cattle. This improvement has been very slow, and it was accomplished largely before there was any exact knowledge of heredity. The lack of consistent direction in breed development has hampered the rate of improvement severely. The improvement attained in present-day breeds of

livestock is largely attributed to selection. Although it is impossible to say how much selection has been practiced in shaping our present breeds, it is safe to say that it has been a major factor.

Since the discovery of the laws of inheritance, new breeds of livestock have been developed in the short period of about ten years. Selection has played an important rôle in the development of these lines, and they have been developed to preconceived specifications by the deliberate crossing of previously existing breeds and then breeding and selecting on the basis of performance from within those populations. This last line of evidence is a real reason for optimism among breeders of livestock. It demonstrates that animal improvement through breeding and selection can be accomplished in only a fraction of the time required for the formation of the original breeds.

Complications of Selection. If selection were *always* effective, the animal breeder's problems would be largely solved. The reasons listed above are ample justification for carrying out a program of selection, but the many failures of selection serve to dampen the enthusiasm of many people engaged in animal breeding. The complications of selection can be classified as two basic types: genetic and operational, although the distinction may not always be clear-cut. Of the many topics under each of these main headings, some of the main ones can now be discussed.

Genetic Complications of Selection. *Heredity and Environment.* Most characteristics of economic importance in animals are controlled by many genes; the same traits are also greatly influenced by environment. An animal with a fast growth rate, raised on a deficient diet or in an otherwise faulty environment, may end with the same growth rate as an animal that has a poor genetic constitution for rate of growth, but was raised in a good environment. This effect of environment can be responsible for mistakes in selection. It is important, therefore, to have a standard and suitable environment for the stock under selection (Winters, 1938). A suitable environment is one in which the better genotypes have a chance to express themselves. For example, an animal with a genotype for a fast rate of gain will be able to express itself fully only if its nutrition is adequate for fast growth. In a suitable environment the animals with the better heredity will be more likely to be selected for breeding.

Both heredity and environment are responsible for the development of a character. The relative determination of a character by either will vary from case to case, and over a period of time. The important thing for the breeder is to be able to recognize the differences that are hereditary, and thus increase the accuracy of his selections.

Genotype and Phenotype. The genotype of an animal is the animal's genetic constitution. It is more than the sum of all its genes, for it also includes the particular combination and arrangement of those genes. A particular gene will have different effects in different genic combinations. The genotype of an animal can therefore be referred to as its genetic environment (Waddington, 1939). The genotype remains constant for an animal throughout its life.

The phenotype of an animal is the result of the interaction of the genotype and the environment in which the animal is developing. It is the expression of the animal's whole set of characteristics at a particular time. The phenotype, unlike the genotype, changes with time. This affects selection. For instance, phenotypic selection of rams and ewes should be done when they are at a market weight, if they are selected as breeding animals for the production of market lambs.

Difficulties in selection arise because we cannot identify the genotype of an animal accurately enough. If we knew exactly the transmitting abilities of our animals, progress from selection would surely follow. We are not likely ever to know this, even after extensive progeny tests.

Heritability. Most selection processes are based on phenotypic differences. Although we select on a phenotypic basis, our aim is to effect genotypic changes. The amount of change that selection is able to bring about is dependent on the relationship of phenotypic variation to genotypic variation. If the phenotype accurately reflects the genotype, selection will be quite accurate. If most of the phenotypic variation is environmental, progress from selection will be slow.

It has long been recognized that the phenotype represents a combination of genetic and environmental effects (Dempster and Lerner, 1950). The methods of separating these effects have been developed gradually over a long period of time. Wright (1920) was one of the first geneticists to separate the genetic and envi-

ronmental components of phenotypic variation. In these experiments, Wright not only showed the relative importance of heredity and environment in determining the piebald pattern in guinea pigs but also demonstrated the effect of inbreeding on the variability of this trait. He showed that the variability due to heredity was greatly reduced with increased inbreeding.

Wright (1921) also devised a statistical method of separating the genetic and environmental portions of the phenotypic variation by means of path coefficients. These methods have been used as a basis in arriving at estimates of degrees of heritability of various traits (Lush, 1945).

Heritability may be defined as "the portion of the total phenotypic variation which is due to additive gene action" (Lerner, 1950). It is this definition that we are most interested in, because heritability in this sense gives us an estimate of what we can hope to achieve by selection. Heritability is sometimes also defined as the portion of the total phenotypic variation that is due to hereditary differences between individuals (Lerner, 1950). This latter estimate includes genetic variation due to epistasis, dominance, and various other interactions on which selection cannot act effectively. We need to concern ourselves only with the first definition here.

The larger the additively genetic portion of the phenotypic variance, the more accurately will a heritability estimate serve to identify the genotype. For this reason selection will be more effective in herds and for characteristics where the heritability is high.

Heritability estimates are ratios expressed in per cent and are usually designated by h^2 . Like all ratios, the estimates will vary as their components vary. We can show this with an oversimplified example. Let us designate heritability as $h^2 = H/(H + E)$, where H refers to the hereditary variation, E refers to the environmental variation, and H and E together equal the total phenotypic variation.

The hereditary variation, H , can be reduced through inbreeding and increased by an outcross or by a more complete control of environment. In a herd in which the inbreeding of the animals is advancing, the heritability will decrease. After an outcross, the genetic variability and, therefore, the heritability will be raised.

When the animals in a herd are not raised under similar conditions, much of their phenotypic variation will be environmental. This will have the effect of reducing heritability. In our fraction, E will be large, and h^2 will be reduced. Where such a situation exists, many mistakes in selection will be made.

It can now be seen that heritability estimates are based on the variation in a particular trait, at a particular time, and under particular conditions. In spite of these restrictions, the various estimates of heritability for the same characteristics in different herds have shown remarkably close agreement.

These estimates are very useful in appraising the results that we can hope to get through selection. They also indicate when an outcross is necessary to effect further improvement or if more careful control of the environment will be sufficient to increase the heritability. Heritability by itself does not really show when the environmental variation is excessively large. This information can be gleaned from a knowledge of the management practices in the herd and from a study of the analysis of the data used in computing the heritability estimates.

Of the several methods of obtaining estimates of heritability, all have one thing in common: all of them are based on relationship (Lush, 1945). This relationship may be parent-offspring, full-sib, and so on. It is then possible to estimate how similar the genotypes of these relatives are from the closeness of the relationship that is used in making the analysis. A comparison of the variation between these relatives and the variation between less closely related animals in the same herd is the basis of all heritability estimates.

Table IX shows some actual heritability estimates for various characteristics in farm animals.

Regression to the Mean. Many breeders have been frustrated by the observation that the offspring of the animals that they selected had a tendency to regress to the average of the breed from which they were selected. Galton first pointed this out when his studies on the height of people showed that tall parents tend to have children that are shorter than the parents, and vice versa. This tendency to regress to the mean became known as Galton's law of filial regression. This tendency confused the early breeders, but it need not confuse us now.

TABLE IX. HERITABILITY ESTIMATES OF TRAITS IN FARM ANIMALS

Class of Stock	Trait	Heritability, Per Cent	Source
Swine-growth rate	Birth to 180 days	30-40	Whatley (1942)
Swine-growth rate	Gains to 56 days	15	Hazel, Baker, & Reinmiller (1943)
Swine-growth rate	Gains 56-112 days	28	Hazel, Baker, & Reinmiller (1943)
Swine-growth rate	Gains 112-168 days	17	Hazel, Baker, & Reinmiller (1943)
Swine-growth rate	Gains 56-84 days	18	Nordskog, Comstock, & Winters (1944)
Swine-growth rate	Gains 56-112 days	28	Nordskog, Comstock, & Winters (1944)
Swine-growth rate	Gains 56-140 days	39	Nordskog, Comstock, & Winters (1944)
Swine-growth rate	Gains 56-168 days	45	Nordskog, Comstock, & Winters (1944)
Swine-growth rate	Birth to 200 pounds	21	Nordskog, Comstock, & Winters (1944)
Swine-growth rate	56 days to 200 pounds	40	Nordskog, Comstock, & Winters (1944)
Swine	Fertility	5-15	Pearson (1911)
Swine	Fertility	17	Rommel & Phillips (1906)
Swine	Fertility	26	Johansson (1929)
Swine	Fertility	14	Lush <i>et al.</i> (1933)
Swine	Fertility	17	Lush & Molln (1942)
Swine	Fertility	17	Stewart (1945)
Swine	Fertility	33-44	Henke (1935)
Dairy cattle	Milk production	20	Lush, Norten, & Arnold (1941)
Dairy cattle	Butterfat production	30	Lush, Norten, & Arnold (1941)
Dairy cattle	Butterfat production	14-17	Lush & Strauss (1942)

Poultry	Egg production	20-25	Monroe (1936)
Poultry	Egg production	31	Monroe, Bud, & Hopkins (1937)
Poultry	Egg production	22.5	Lerner & Taylor (1943)
Poultry	Egg production	33	Shoffner (1946)
Poultry	Intensity of egg production	21	Lerner & Taylor (1943)
Poultry	Persistency of egg production	5	Lerner & Taylor (1943)
Poultry	Non-pause egg production	10	Lerner & Taylor (1943)
Sheep	Type	13	Hazel & Terrill (1943)
Sheep	Condition	4	Hazel & Terrill (1943)
Sheep	Breed type	15	McMahon (1943)
Sheep	Fleshing	13	McMahon (1943)
Sheep	Score for type	12	Hazel & Terrill (1943)
Sheep	Weaning weight	30	Hazel & Terrill (1943)
Sheep	Staple length	40	Hazel & Terrill (1943)
Beef cattle	Birth weight	34	Knapp & Nordskog (1946)
Beef cattle	Weaning weight	30	Knapp & Nordskog (1946)
Beef cattle	Final feed lot weight	94	Knapp & Nordskog (1946)
Beef cattle	Gain in feed lot	97	Knapp & Nordskog (1946)
Beef cattle	Efficiency of gain	48	Knapp & Nordskog (1946)
Beef cattle	Birth weight	53	Quesenberry (1951)
Beef cattle	Weaning weight	28	Quesenberry (1951)
Beef cattle	Weight at 15 months	86	Quesenberry (1951)
Beef cattle	Rate of gain on feed	65	Quesenberry (1951)
Beef cattle	Weaning score	28	Quesenberry (1951)
Beef cattle	Slaughter steer grade	45	Quesenberry (1951)
Beef cattle	Carcass grade	33	Quesenberry (1951)
Beef cattle	Area of eye muscle	68	Quesenberry (1951)

This regression can now be explained fairly easily. When we get animals that are outstanding in characteristics such as rate of growth, economy of feed, and so on, it is probably because these animals happened to get a favorable combination of genes and a satisfactory environment for these genes to express themselves. When these animals in turn reproduce, new combinations of genes are formed through segregation and independent assortment, and these usually will be more like those of the average of the breed. The gene combinations giving rise to exceptional individuals are themselves rare. Furthermore, the environments in which these individuals develop are also exceptionally good. The extreme animals, through the chance association of rare gene combinations and a rare environment, appear to be better than their actual breeding worth. Similarly, the poorer-appearing animals are probably better in breeding value than their appearance indicates.

The genetic part of the regression can be at least partly avoided by increasing the homozygosity or genetic purity through inbreeding. The more nearly pure an animal is genetically, the less segregation there will be. Naturally, where the heterozygote is superior to either homozygote, it will not be possible to fix this superiority. In such cases, the systematic crossing of lines is the only way to restore superiority.

The environmental part of the regression can be lessened a great deal by keeping the same environment as far as possible from year to year. This is another reason for testing animals under conditions similar to the ones in which they or their offspring are to perform. It is not likely that the very best animals will be made homozygous even through inbreeding, but their breeding value will be improved somewhat in proportion to the amount of the purification achieved. A clear understanding of the causes for regression of offspring to the breed average will be a great help in a breeding program.

Types of Gene Action. The fact that genes act differently in different combinations may make accurate selection more difficult. A simple case of dominance in a single gene pair will illustrate the point. Where A is dominant to a , AA and Aa individuals will be of the same phenotype. They will be selected with equal preference, but AA will breed true whereas Aa will segregate.

In the case of overdominance, Aa will produce a larger effect than AA or aa . Here selection will favor the heterozygote, Aa , which can never be fixed. As stated previously, crossing of appropriate inbred lines should produce overdominance effects, if the condition exists.

Where there are many alleles in a series, combinations of some of them will produce more favorable effects than others. For example, in a series, A_1 , A_2 , A_3 , and so on, A_1 and A_3 may produce a more favorable effect than any other combination. The job of the breeder here is to increase the frequency of the favorable alleles and to discard the less favorable ones. Selection with inbreeding should accomplish this.

In interactions of genes that are not alleles, a gene may complement or inhibit the action of another gene or group of genes. We do not know all the ways in which genes interact to produce an effect, nor do we know the frequency of such interactions. We do know that for the breeder the net effect of non-additive gene action is that he cannot hope to combine all the desirable effects into one super line or breed. The breeder will do better to develop numerous lines that produce relatively well, and then systematically cross those lines that produce the highest-performing crossbreds. Developing successful lines and finding suitable combinations for crossing can go on even though the type and frequency of gene interaction remains unknown. The methods are known, and the results are gratifying.

Correlation of Traits. Some characters are genetically correlated. For example, it has been shown that a rapid rate of gain in swine is positively correlated with efficiency of gain (Fine, 1951). Other characters are negatively correlated. In the case of positive correlations between desirable traits, selection is made somewhat easier, because selection for one automatically selects somewhat for the other.

Negative correlations between two desirable traits, or positive correlation of desirable with undesirable traits, have the same effect. They tend to lessen the effectiveness of selection. Wherever possible, undesirable associations should be broken up by crossing, inbreeding, and selection. Many such undesirable associations probably cannot be broken up because of their physiological basis. In other cases, it should be possible to break up unfavorable associations and bring about more favorable ones.

A knowledge of the correlations between various characters should be a great help in avoiding mistakes in selection.

Effects of Inbreeding. It is generally known that a decline in all the attributes of vigor usually accompanies inbreeding. Hence many breeders hesitate to practice inbreeding. Inbreeding, however, is necessary to induce gene segregations and to fix desirable gene combinations. In the words of Wright (1939), "The only method by which selection can be brought to bear effectively on the rare favorable recessives to increase their frequency, or on rare unfavorable ones for their elimination, is by inbreeding."

Several positive steps can be taken to counteract the depressing effect of inbreeding on vigor. The first step is to choose foundation animals that are superior in production. Rigid selection should be followed from the outset so as to offset the effects of inbreeding on performance.

The system of inbreeding employed should be a flexible one, so that the opportunity for selection is increased. If fixed systems of mating, such as brother-sister, sire-daughter, etc., are followed, it will often be impossible to mate the best-performing males with the best-performing females. Furthermore, such fixed systems will make it impossible to use certain exceptional sires to the extent to which their merit dictates that they should be used. Some fixed systems of mating will advance the inbreeding so rapidly that maximum segregation will not be promoted, and selection will have no opportunity to act. With a flexible system of mating, the rate of inbreeding can be more easily controlled, and geared to the selection program.

Animal breeders often use the term "prepotency." Prepotent individuals come about through inbreeding. Prepotency is the regularity with which parents transmit their characters to their offspring. Regularity of transmission is increased with increased homozygosity, which is obtained only through inbreeding and selection.

Operational Complications of Selection. *Objective in Selection.* Many failures of selection in livestock can be attributed to a lack of definite objective. Examples of this can be found in every class of stock where there has been selection for type. The most popular type one year has met with disfavor a few years later. As a result of this, selection has changed direction frequently, and real progress has been slow or entirely lacking.

The direction of selection changes most frequently where the objective is evaluated by judgment rather than measurement. The reason probably is that the breeders themselves do not agree on the objective or else have only a hazy idea of what their objective is. Defining the objective by measurements clarifies the problem, and tends to bring about closer agreement among breeders.

Selection will be more effective when the breeder has a definite objective for which to strive. This objective must be defined by measurements. There will still be ample opportunity for the breeder to exercise judgment. This judgment should be used along with measurements, but should never replace measurements.

Number of Traits. Selection becomes increasingly complex as the number of traits under selection increases. When a single trait is subjected to selection it is a simple matter to rank the individuals in the order of their merit for that trait. This becomes more difficult as the number of traits is increased. An individual may be very good in one character but deficient in the others. Very few animals will be good in all the characters that are under selection. Animals must be selected as a unit, and, when an individual is selected for a character in which it excels, all its other characters are also selected. This will result in selecting animals that are lower on the scale of merit in some traits because they are particularly good in one or more of the other traits. To simplify this problem, the number of traits must be kept as small as is practicably possible. The traits put under selection must be those with the greatest value from the standpoint of utility.

Foundation Stock. Selection may be ineffective because of an unfortunate or unwise choice of foundation stock. If the foundation animals are genetically poor, no one has as yet demonstrated that selection pressure will be effective in bringing about improvement within a reasonable or workable period of time. Selection merely sorts genes, and permits the better ones to be saved and the poorer ones to be discarded. Therefore it is very important to start with good foundation stock. If the genes that we are looking for are not in the foundation animals or are very infrequent, they will have to be introduced by crossing, or selection will be powerless. Selection can act only when there is varia-

bility. Genetic variability is caused by heterozygosity, and can be increased by outbreeding. Selection is ineffective for loci that are already homozygous.

Level of Performance. Sometimes selection may be effective for a while, and then it becomes ineffective for further progress. For example, in artificial breeding centers where proved dairy sires are used, it is easy to raise milk production in herds with low production. After several generations, as the level of performance of these herds is raised, further progress will become less and less. Selection here will lose effectiveness, not because the quality of the sires is lower, but because the level of performance of the cow herds has become higher. When the level of performance of a line is already high, further progress by selection will be slow, unless it is accompanied by a system of mating that will bring about new gene combinations.

Systems of Selection. Too much rigidity in the *systems* of selection may be a handicap to progress in an animal breeding program, just as a fixed system of mating is sometimes harmful. If the relative importance of each character was known exactly, a fixed system of selection might serve very well. This information is not known exactly, and it varies from herd to herd and from one situation to another.

If a line is deficient in a certain trait, the maximum selection should be applied to that trait. Comstock and Winters (1944) showed that inbreeding affected fertility more than rate of growth. In the Minnesota work, therefore, more selection has been directed to increasing fertility. This probably could be taken into account in a selection index, but many of the traits vary in importance from year to year, and with the availability of the material on hand. A selection index that is correct on the average, over a period of years, is not good enough. The system of selection should be flexible enough to allow the maximum selection to be applied where the need is at any particular time. Furthermore, selection indexes have been proposed for some time and no one has yet demonstrated ability to use them effectively in the improvement of livestock.

A fixed standard of selection, such as a minimum record of performance, also has definite complications. A breeder may specify that no pigs should be selected from litters with less than eight weaned, but there will be years when there are too few

litters of eight or more for selection to operate on such things as rate of growth and feed efficiency.

Length of Time. In order to effect improvement of livestock through selection, a breeder must be prepared to continue his project for a relatively long period of time. The turnover in livestock is slow in terms of numbers of animals, and in numbers of generations. Progress of a single generation is apt to be completely masked by environmental effects, and it takes many years to turn over several generations in larger classes of livestock. Although progress per year is small, real improvement can be effected over a longer period of time.

Number of Animals. When the number of animals in a line or herd is small, selection is severely restricted, because small herds or flocks offer so little opportunity for genetic segregation. There can be little selection in such cases. Even in less extreme cases, selection is likely to be handicapped through a lack of numbers.

Selection in Small Animals. Selection experiments with laboratory animals have been numerous. In *Drosophila*, selection has most often been for bristle number (Mather, 1949; Sismanidis, 1942; Heuts, 1948). In mice, selection has been for white hairs and body size (Goodale, 1938; MacArthur, 1949). In rats there have been selection experiments for hooded pattern (Castle, 1951) and for efficiency of food utilization (Morris, Palmer, and Kennedy, 1933). The experiment reported by MacArthur (1949) on selection for body size in mice seems to be typical of the selection experiments in small animals. It will be discussed briefly to indicate how selection has operated in the laboratory.

MacArthur (1949) reported on a selection experiment for large and small body size in mice. The report covered 21 generations of selection. The foundation stock consisted of animals produced by intercrossing 6 inbred strains of mice of average size, but of various colors.

In carrying out his selections, MacArthur identified and weighed all the mice individually. The actual selections were made by comparing the weight of individuals and sibships with their parents and sometimes with their progeny. He did not draw sharp distinctions between individual, pedigree, and progeny selection. His pairings of large mice were made at random within one closed population, using one male with several females.

The same practice was followed in the small line. The more or less random mating slowed advance in the rate of inbreeding. Pairs that produced first litters of promising body size were mated again to multiply favorable genotypes.

With this type of selection MacArthur succeeded in completely separating a large and a small line of mice. The smallest mice in the large strain were bigger than the largest mice in the small strain. The actual weights of the large and small mice for 0, 7, 14, and 21 generations are shown in Table X.

TABLE X. SIZES (BODY WEIGHTS IN GRAMS AT 60 DAYS) OF MALE AND FEMALE HOUSE MICE FROM THE UNSELECTED STOCK (GENERATION 0) AND FROM SMALL AND LARGE RACES AFTER 7, 14, AND 21 GENERATIONS OF PLUS AND MINUS SELECTION

(MacArthur)

Genera- tion	Male			Female		
	Mean Weight	Standard Deviations	Coeffi- cient of Varia- bility	Mean Weight	Standard Deviations	Coeffi- cient of Varia- bility
L-21	39.85 \pm 0.47	5.10	12.80	34.46 \pm 0.49	5.12	14.86
L-14	36.79 \pm 0.37	3.66	9.95	30.71 \pm 0.31	3.29	10.71
L-7	34.69 \pm 0.37	3.59	10.34	27.51 \pm 0.39	3.80	13.81
0	23.16 \pm 0.26	2.56	11.01	19.51 \pm 0.25	2.65	13.52
S-7	17.25 \pm 0.30	2.61	15.13	13.56 \pm 0.27	2.34	17.36
S-14	13.93 \pm 0.23	2.13	15.29	11.69 \pm 0.20	1.74	14.89
S-21	11.97 \pm 0.28	1.71	14.29	10.79 \pm 0.26	1.47	13.62

The bulk of the change in body size had already occurred by the end of 7 generations. The later changes came more slowly, and the heritability of body weight decreased from about 25 per cent to about 10 per cent. The total variability of the mice was about the same at the start of the experiment as it was at the beginning. The heritability figures indicate that much less of the variability was genetic.

Conscious selection was carried on for body weight only, yet several correlated responses took place. The two races of mice differed in coat color, relative size of appendages, temperament, and litter size. Several possible explanations for the correlated responses are suggested by MacArthur. Some of the genes with neutral effects for growth probably drifted apart at random. Some color genes may also have an effect on growth rate. Such multiple effects of a gene are called pleiotropy.

Relative growth of various parts may have caused the larger relative size of appendages in the small mice. Different rates of change in body surface to body weight may have had an effect on metabolism so as to change the animal's temperament. Litter size and growth may have been correlated through the endocrines. Linkage may have been responsible for some of the correlated responses.

The results of this experiment are explained in very simple terms. MacArthur states, "The job was to re-shuffle the size genes, and unpack and reorganize the chromosomes to bring together as many plus genes as possible in the large race." It seems that the chromosomes with the most plus genes for body size were sorted into the large race of mice, and the ones with the most minus genes into the small race. This occurred early when most of the progress was made. Later progress was slower, and was made possible by recombinations of chromosomes through crossing-over, bringing still more plus genes together in the large race, and vice versa.

Mather (1949) explains the results of his selection experiments with *Drosophila* in a very similar way. He refers to the plus and minus genes as polygenes. This term is frequently used in relation to the inheritance of quantitative characters. Many polygenes with small effects are postulated. Some of these polygenes have negative and some have positive effects. If the plus and minus effects are equally distributed over the chromosomes, their net effect is neutral. In selection experiments, when plus (or minus) polygenes are sorted out, the effect is quite appreciable.

It can be seen that selection in small animals can be very effective, and that the genetic explanation of the results is relatively simple. Why then can we not get such spectacular results in farm animals? One reason is that we are forced to select for many more characters in farm animals. In laboratory animals selection can be concentrated on one character, but in farm animals utility is based on too many characters to make this possible. Furthermore, farm animals have been under artificial selection for so many generations that much of the original variability of some characters may have become fixed, although the variability in economic characters appears to have remained rather large.

Large numbers of small animals can be maintained in the laboratory at a moderate cost. In livestock the numbers of animals must be kept relatively small because of the cost of maintaining them on an experimental basis. The generation interval is much longer in farm animals than it is in the small animals. MacArthur's mice averaged about three generations per year. In swine, a generation is at least a year, and ordinarily much more. In sheep and cattle the generations are even longer, and the number of offspring per dam is smaller. We must be prepared to spend many more years on selection experiments with our farm animals in order to show improvement comparable to that demonstrated in laboratory animals over a very few years.

Selection in Swine. Published results of selection experiments with swine are now becoming available. Most of these reports come from the various cooperating stations in the Regional Swine Breeding Laboratory setup. For the most part these reports are based on data that have been gathered in the formation of inbred lines rather than from experiments designed specifically for the study of selection.

Dickerson and Hazel (1942) compared various methods of selection for 180-day weight on the basis of expected rate of improvement. They found, "Progress is nearly maximum when gilts are selected on 180-day weight and the dam's productivity and all gilts are replaced annually." This seems to contradict MacArthur's suggestion that mating parents who have produced a good first litter will "multiply favorable genotypes." More studies will have to be conducted to determine how far the shorter generation interval, when only gilts are saved, will compensate the good effects of increasing favorable gene complexes by saving the exceptionally good females (and males) for additional litters.

Krider *et al.* (1946) reported on a selection experiment for rapid and slow growth rate in swine. They succeeded in separating two lines, but concluded that the separation was due mainly to the decline in gaining ability in the slow line rather than to any improvement in the rapid-gaining strain. At the time of their report, the experiment had not been carried out over enough generations to draw many conclusions. The records of gilts for four years were reported. Year to year differences in environment over such a short period could have a marked effect on the

results. That the two lines were separated seems to indicate that selection does have an effect even over short periods of time.

Dickerson and Grimes (1947) studied the effectiveness of selection for efficiency of gain in swine. The results indicated "that selection based on rate of gain from weaning to market weight would be nearly as effective in improving economy of gain as selection based directly on individual requirements for feed." Selection for high and low feed efficiency was successful in separating the two lines.

Laben and Whatley (1947) made a study of selection in an inbred line of Duroc swine. The study of data covering 6 generations of a closed population showed that the performance of the line declined steadily, although the selected animals each year were considerably superior to the average of their generation.

Kottman *et al.* (1948) reported a selection study with inbred lines of swine. They found the annual selection differentials to be one-fourth of a pig per litter at birth, one-half of a pig per litter at weaning, and 18 pounds in individual weight at 154 days. In spite of this amount of selection, the level of performance of the lines was below the expected performance when allowance was made for a decline from inbreeding, and for improvement from selection.

Bernard *et al.* (1950) studied the usefulness of a selection index for swine on Wisconsin farms. The characters included were number farrowed, number weaned, number at 154 days of age, individual and litter weights at weaning and at 154 days of age. The gilts recommended by the use of the index differed significantly from those gilts not recommended, but still selected, for all characters included in the gilts' own selection index.

On the whole, these reports are not nearly so hopeful as those on selection in smaller animals. The selection studies of the Minnesota data are more optimistic and are reported following the presentation of the methods of selection at Minnesota.

Demonstration of the Use of Minnesota Swine Records. Every pig is identified at birth by ear notching. The litters are numbered by tens, proceeding from litter 0 to litter 990. The numbers are then used again, but the letter A is put in front of the numbers. These litters read A0 to A990. The next round of numbers is preceded by B, and so on. The letter is not indicated on the ear, and, because pigs are relatively short-lived,

very few pigs with the same number will be in the herd at the same time. The few that do happen to have the same number can be identified by their difference in age.

The notches used in this system of numbering are shown in Fig. 49. No one pig will have all these notches. Individual descriptions and illustrations of the notching and numbering are presented in Figs. 50 to 55.

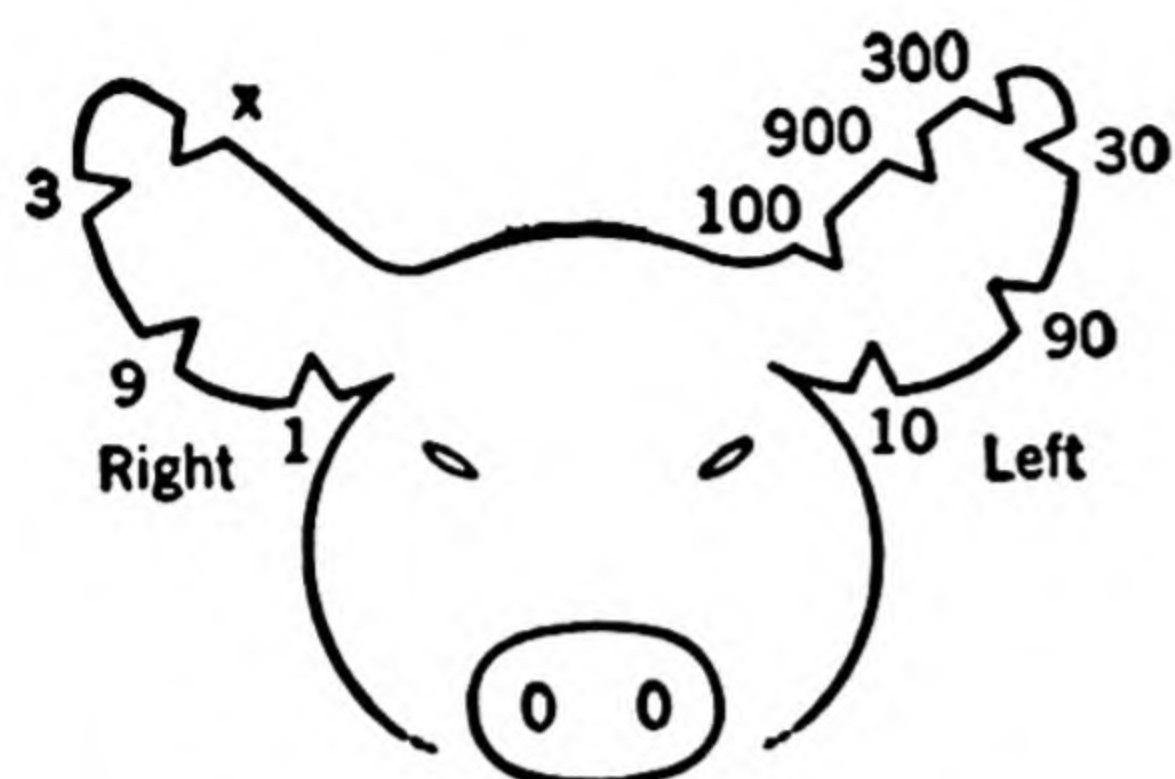


FIG. 49. All the notches used in a system numbering individually.

The pigs within a litter are numbered individually. For example, in litter 0, the first pig is 0 and has no ear notch. The rest of the pigs are numbered 1, 2, 3, and consecutively to as many pigs as there are in the litter. It is a good practice to notch all pigs of one sex first

and then those of the other. It does not matter whether males or females have the lower numbers, so long as the same procedure is followed in each litter. In a litter of 4 males and 5 females, the males will be 0, 1, 2, and 3 and the females will be 4 through 8.

The herdsman's book is most important for the collection of good records. This book should be of such a size and quality that it can be carried in the herdsman's pocket without loss or

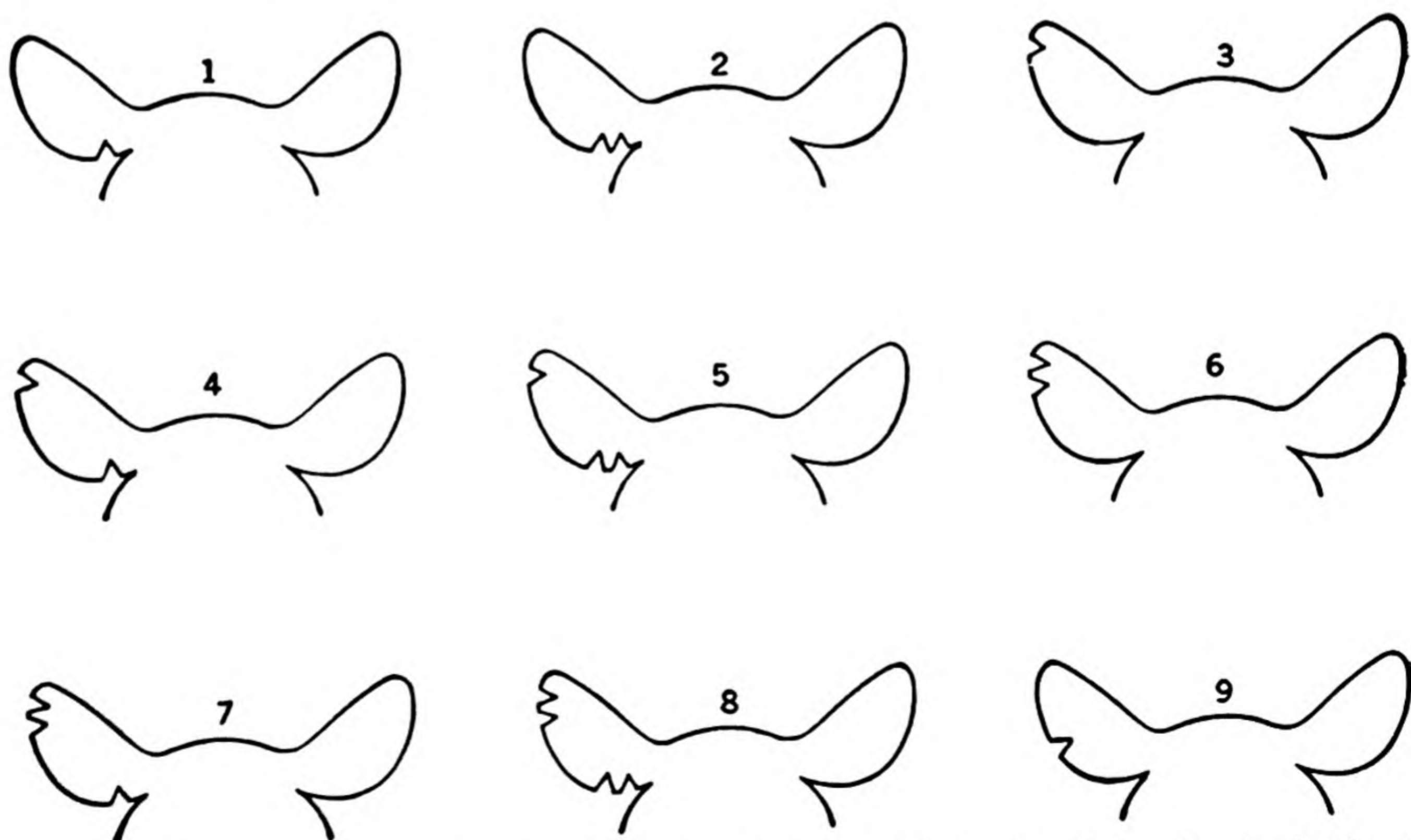


FIG. 50. The individual ear notches used for litter 0. The first pig in the litter is 0; hence it has no ear notch and no illustration is included.

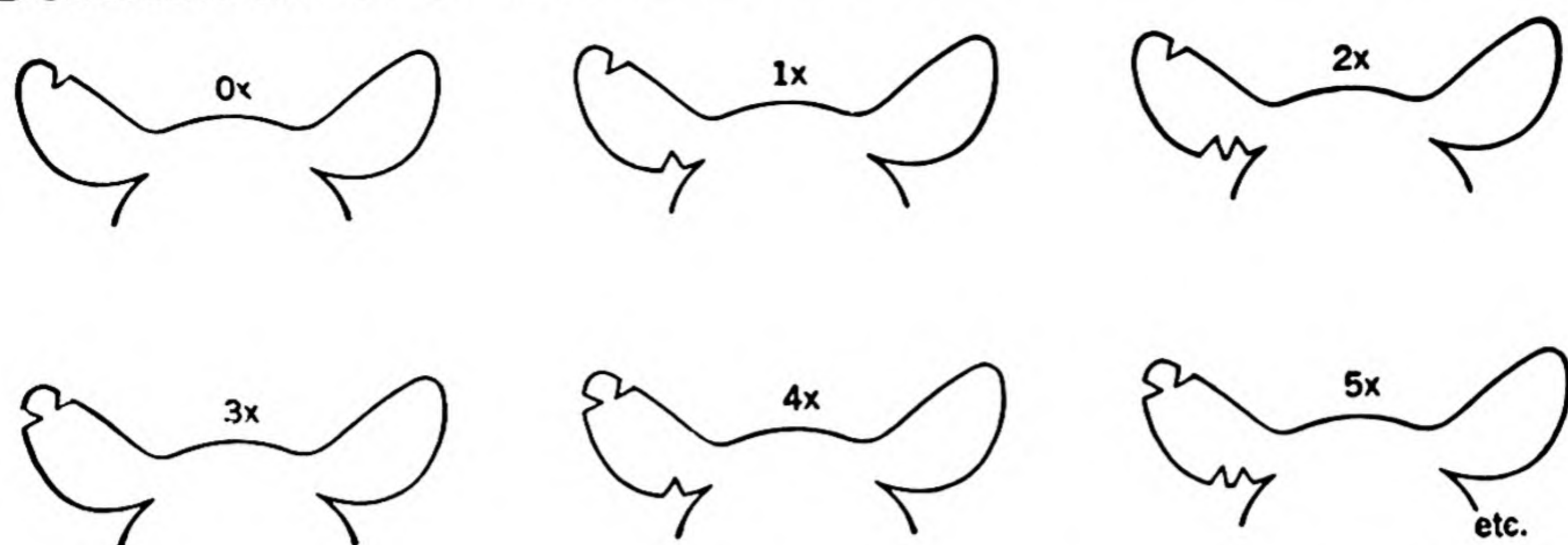


FIG. 51. The identification of pigs when there are more than 10 in the litter. The eleventh pig is 0X, the twelfth, 1X, etc.

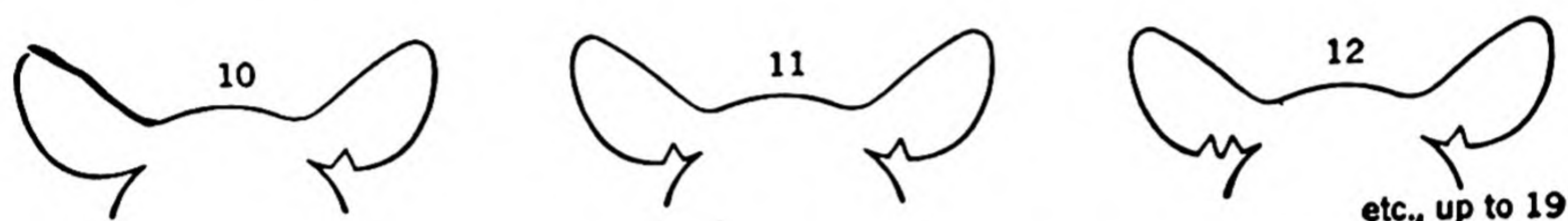


FIG. 52. Litter 10. The notch for 10 indicates the litter number. The individual pigs are numbered as shown. If there are more than 10 pigs in the litter those after number 19 are marked with an X notch as indicated in Fig. 51, except that in this case the litter notch 10 is used.

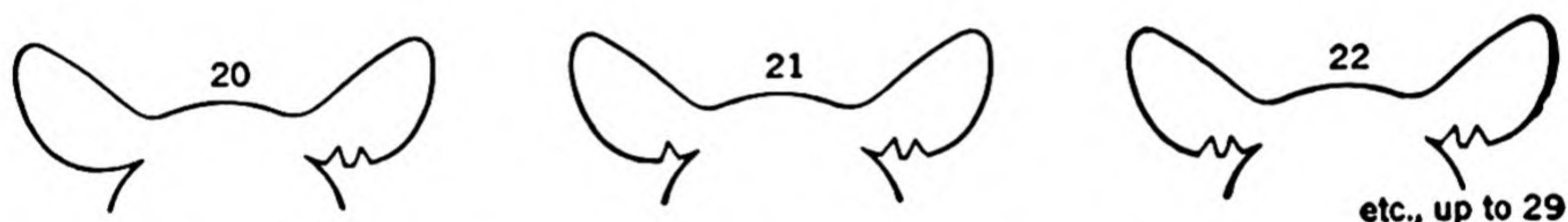


FIG. 53. Litter 20. The notch for 20 indicates the litter number, and the individual numbers are as shown. In case there are more than 10 pigs in the litter, the X notch is used as indicated in Fig. 51.

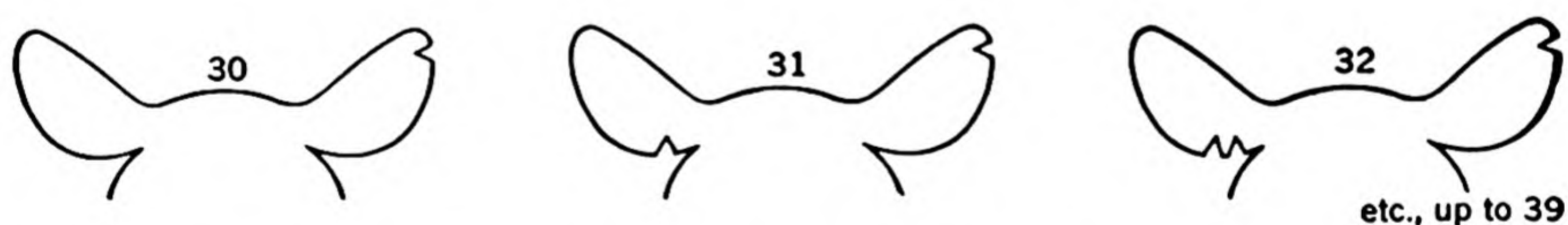


FIG. 54. Litter 30. The notch for 30 indicates the litter number. The individual pig numbers are as shown.

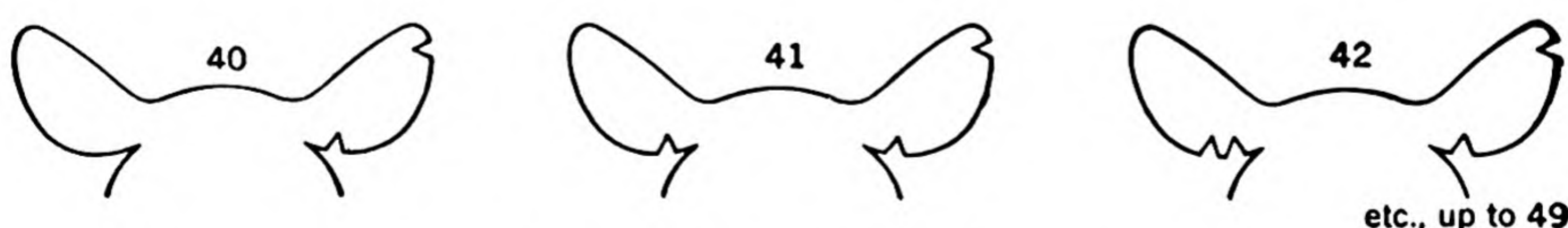


FIG. 55. Litter 40. The litter number 40 is indicated by a 30 and a 10 notch. Individual pig numbers are as shown.

damage to the pages. At Minnesota this book is used to record all the breeding information. The sire and dam are listed, along with the weight of the sow at breeding, farrowing, and weaning. The date of breeding is also recorded. The individual pigs are listed at the time they are ear-notched, along with their birth weight, sex, and condition at birth. Later the dates of vaccination and weaning are noted in this book. The deaths of any pigs are recorded as they occur. Any other information that concerns either individual pigs or litters is recorded. Finally the weaning weights of the individual pigs and the date of weaning are listed.

The herdsman provides a list of all his matings to the central office, so that litter pedigrees can be made up even before the litters are born. As the information becomes available, the litter number, date of birth, number of pigs born alive, and the number of males and females weaned are entered on the previously prepared pedigrees. The inbreeding of the litter is entered as soon as it is computed.

A preweaning sheet is filled out by the herdsman and sent to the central office for processing. These data are directly transcribed from the herdsman's book, and include the weaning weights and all the information preceding weaning. Figure 56 is a completed preweaning sheet for litter F920.

At weaning, the larger litters are placed in a test lot on pasture. Each test lot is about a quarter of an acre of pasture, and has a portable shelter, a self-feeder, and a waterer. Since sufficient test lots are never available to test the entire pig crop, only the larger litters are put on test. Each of these larger litters is placed in a separate lot. This first stage of selection is based entirely on litter size. This insures that any pig selected from test litters will be at least fair in litter size. Litter size is most affected by inbreeding, and is important enough to warrant the strict attention that it receives. The proportion of litters put on test varies from year to year but approximates from 40 to 60 per cent. This is the first round of selection; the average weight of the pigs selected is about the same as that of the unselected, sometimes more and sometimes less.

When a litter is designated as a test litter, the whole litter is placed on test. This makes it possible to practice individual

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selection within the litters, as well as litter selection. In some cases, a single exceptional individual may be selected from an

A.H. Form 484 UNITED STATES DEPARTMENT OF AGRICULTURE
Bureau of Animal Industry
Regional Swine Breeding Laboratory
Cooperating Station North West Station

LITTER RECORD, FARROWING TO WEANING

Sow number F162 Litter number F920
Sow's sire E673 Sire of litter E660
Sow's dam E270 Breeding of litter Minn. #2
Inbreeding of sow .28 Inbreeding of litter .33
Date of birth, sow 3-4-50 Farrowing date 3-21-51
Litter 1ST Date vaccinated 5-29-51
(1st, 2nd, etc.) Date weaned 5-18-51
Sow's weight: at breeding _____
at 109-112 days _____
at weaning _____

Sow's general appearance:
at farrowing: Good, Medium, Poor
No. good teats: R _____ L _____
at weaning: Good, Medium, Poor
No. functioning teats: R _____ L _____

Litter's general appearance:
at farrowing: Good, Medium, Poor
at weaning: Good, Medium, Poor

Pig No.	Sex	Birth Weight (lbs.)	At 56 Days ^{1/}		Disposal at Weaning	Remarks, Defects, and Abnormalities
			Weight (lbs.)	Score		
F920	F	3.0	46			
F921	F	2.0				Died 4-5-51
F922	F	1.8	31			
F923	F	1.5				Died 4-14-51
F924	M	1.7	31			
F925	M	1.6	40			
F926	M	2.5	33			
F927	M	2.0				Died 3-25-51
F928	M	2.1				Died 4-16-51
F929	M	2.4	44			
F920X	M	2.8	44			
F921X	M	3.0	36			
		1 born dead				

^{1/}Type, conformation, symmetry, and breed characteristics including color, scale.

FIG. 56. A preweaning swine record.

otherwise ordinary litter. In other cases an entire litter may be selected, if the litter record is good enough.

This system is deliberately different from the ones in which only a sample of the litter is tested. If the pigs are appropriately

selected, four pigs on test can provide litter information almost as accurate as if the whole litter were tested (Lu, 1951). The information from part of a litter is adequate for sow testing, but it restricts individual pig selection. Testing part of the litter reduces the test to average figures for the litter, and selection can be mostly between litters. Where considerable emphasis is on individual selection, the whole litter needs to be tested. In this way selection can operate on the variation within litters.

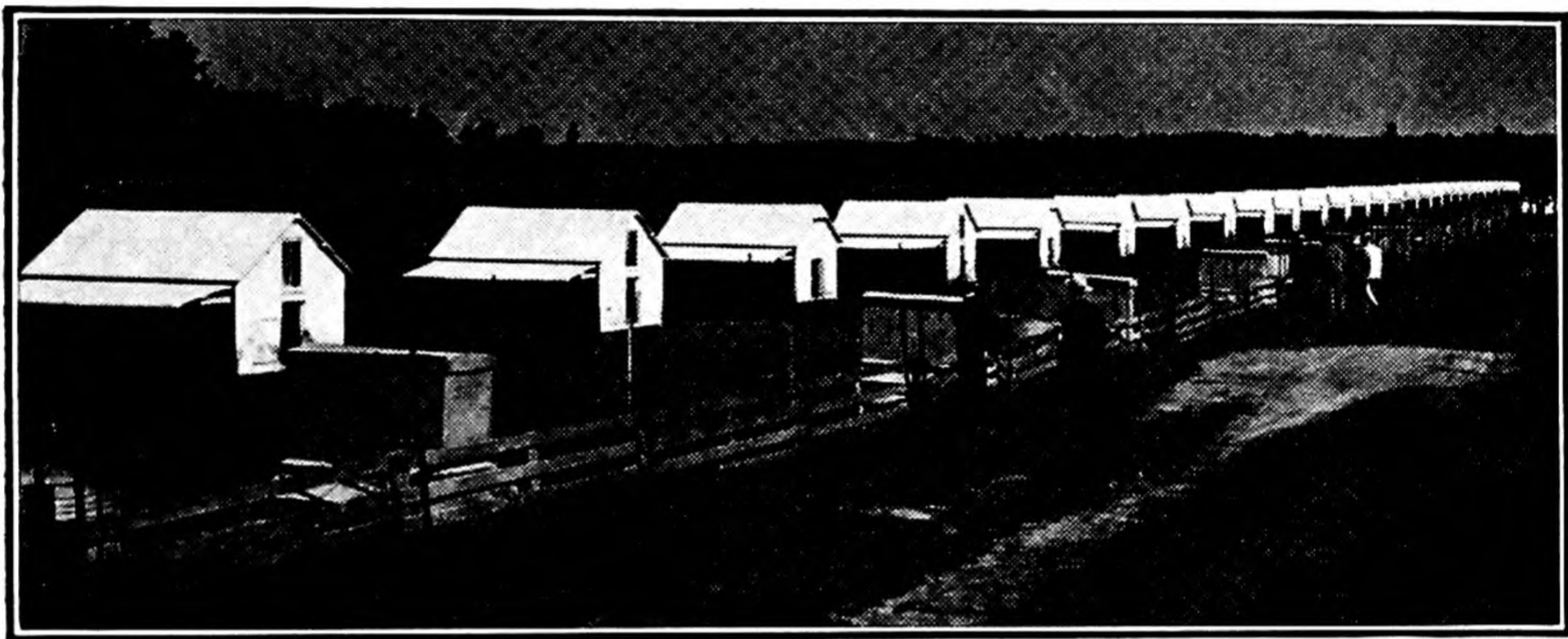


FIG. 57. Swine litter test lots.

The pigs of test litters are weighed individually at 84, 112, 140, and 154 days. The feed records are kept on a litter basis. There are four feed periods, corresponding to the weighing dates as follows: first period, 56 to 84 days; second period, 84 to 112 days; third period, 112 to 140 days; fourth period, 140 to 154 days. The ration is highest in protein for the first period and lowest for the fourth period. The corn content of the ration is increased in each successive period. The weigh sheets and feed sheets are kept by the herdsman, and a copy of each is submitted to the office for processing.

The pigs are individually scored on the day they are weighed out of the test lots. This score is assigned on the basis of eye appraisal. It consists of an over-all appraisal of the pig as to type, constitution, and possible physical defects. The values for score range from one through nine. The top score is nine, and is reserved for individuals that are excellent in the scorer's opinion. This is standard procedure for all cooperating stations in the Regional Swine Breeding Laboratory.

When all the field records are in, they are processed and entered on litter summary sheets. Figure 58 is a completed litter summary sheet for litter F920. The litter summary sheets are used in making the actual selections. They contain all the information on the factors of performance that are used as criteria for selection.

The factors of performance that are used for selection are:

- Number of pigs farrowed alive
- Number of pigs weaned
- Weight at 154 days
- Rate of gain from 56 days to 154 days
- Economy of gain
- Body score

Weight at 154 days and rate of gain from 56 days to 154 days together constitute the criterion for growth rate. Economy of gain is measured as the feed consumed per hundredweight gain.

Although 154-day weights are used as the end period here, any other suitable period can be used. Whatever end period is chosen, it is important that it be strictly adhered to.

The litter summary sheets of the tested litters are first sorted according to litter size at birth and at weaning. Gilts and boars are then selected from the larger litters on the basis of their growth rate, body score, and economy of gain. The amount of superiority of selected individuals over the line average is never specified in advance. The proportion to be saved and the superiority of those saved depend on the availability of material in any particular season. The best-performing pigs are saved for breeding each year.

There is considerable flexibility at various points in the selection program. First, the different characters are not assigned particular values and combined into one composite score. This allows the amount of selection for the various characters to fluctuate from year to year and from situation to situation. In this way a concentration of selection for growth rate may be applied at a time when it appears that growth rate needs to be improved in relation to the other performance factors. In some instances pigs with exceptional growth rates will be selected, even if their litter size is perhaps below the desired level. Thus, the greatest selection can be applied where there is the greatest need for it.

LITTER SUMMARY SHEET

Litter F920

Station N.W.

Year 1951

Line Minn #2

Date of farrow 3-21-51

F_x of Dam 28

Age of Sire 2 yr

Sire E660

F_x of Litter 33

Age of Dam 13 mo.

Dam F162

	Average	ns ²		1	2	3	4	5	6	7	8	9	OX	1X
Pig No.			F920	F	F	F	M	M	M	M	M	M	M	M
Sex														
No. born alive	12													
- dead	1													
Birth wt.	2.20	3.12	3.0	2.0	1.8	1.5	1.7	1.6	2.5	2.0	2.1	2.4	2.8	3.0
No. weaned	8													
Weaning wt.	38.12	266.88	46	Bied 4/15	31	Bied 4/14	31	40	33	Bied 3/25	Bied 4/16	44	44	36
No. raised	8													
154-day wt.	187.88	1282.88												
- gilts	183.50	760.50	203		164							198	189	204
- males	189.33	471.33					183	182	180					
Rate of gain	1.53	.0773												
- gilts	1.48	.0288	1.60		1.36									
- males	1.54	.0431					1.55	1.45	1.50			1.57	1.48	1.71
Score	7.88	2.88	9		7		8	8	7			8	8	8
Feed per owt. gain	276													

Fig. 58. A completed litter summary sheet.

Flexibility of selection is maintained in the proportion of gilts and old sows that are saved to make up the breeding herd; the proportion depends on the performance of the sows in the herd, based on their ability to raise thrifty litters and on the number of high-performing gilts in the test lots. If a sow has produced a good litter, she is kept in the herd in the hope that the frequency of her genes will be increased in the herd. On the other hand, if a particularly good crop of gilts is available, a larger proportion of these gilts are kept for farrowing.

The selection of boars follows the same pattern as that for females, except that fewer boars are required. For this reason only the more promising boars are left uncastrated to 154 days of age, and the others are castrated early. At times the number of boars selected is kept fairly high, so as not to raise the amount of inbreeding too rapidly. Boars that leave superior offspring are kept as herd sires for several years. The others are replaced annually by young boar pigs.

Standardization of Records. In order to appraise the performance records properly, the conditions under which the records are made must be standardized as far as possible. The pigs are raised as nearly as possible under conditions simulating those in which they will be expected to perform when they go out to producers. The rations and management are kept very similar from year to year.

Some of the records must be adjusted statistically so that they will be directly comparable. For example, sows produce more pigs than gilts do, owing to an age effect on fertility. If this is not adjusted, the gilts will be penalized in selection for litter size. Consequently, age correction factors for number of pigs farrowed have been calculated (Stewart, 1944 and 1945; Fine, 1951). All farrowing records can be corrected to an equal gilt basis. This should help to avoid mistakes in selection for litter size.

Table XI lists the corrections to adjust the farrowing records to a 12-month basis (Fine, 1951). These corrections were derived from Minnesota data. These corrections probably are not generally applicable. Other corrections should be computed for the data where they are to be used.

Pigs are not always weighed at exactly 56 and 154 days. If these weights are not adjusted, the pigs weighed too early will

TABLE XI. CORRECTIONS TO BE APPLIED TO FARROWING RECORDS OF GILTS AND SOWS OF DIFFERENT AGES

Age of Dam, Months	Correction to Number of Live Pigs Farrowed
9	+1.0
10	+0.6
11	+0.3
12	0.0
13	-0.3
14	-0.6
15	-0.8
16	-1.0
24	-1.6
36	-1.0

be penalized and pigs weighed too late will be favored. All the weaning weights are therefore adjusted to a 56-day basis. The formula used for this adjustment is:

$$\text{56-day weight} = \frac{\text{actual weight} \times 41}{\text{age} - 15}$$

All the final weights are adjusted to a 154-day basis by the following formula:

$$\text{Weight at 154 days} = \frac{\text{actual weight} \times 94}{\text{age} - 60}$$

These formulae were derived statistically from a large amount of data (Stewart, 1944; Lu, 1951). These corrections are modifications of those by Whatley and Quaife (1937) and by Bywaters and Willham (1935).

It is usually recognized that heavier pigs eat more feed for maintenance than lighter ones. Feed records based on a definite end period, such as 154 days, tend to favor the lighter pigs. Pigs weighing 160 pounds at 154 days would appear more efficient in feed utilization than pigs weighing 190 pounds at the same age. Some of the lower feed requirements of the smaller pigs are due to their size, and have no bearing on feed efficiency. Kristjansson (1951) studied this condition and devised a method to adjust the feed records to an equal weight basis. All the records are adjusted as though they were made from an equal starting weight

to an equal end weight. These corrections should help in reducing mistakes in selection for economy of gain.

Selection in Sheep. The sheep records kept at Minnesota are quite different from those kept for swine, because the management for sheep is quite different. The records are similar in that both are based on production, and the identity of each animal is kept.

In sheep, each lamb is ear-tagged at birth with duplicate tags—one tag in each ear. In this way a lamb can lose one tag, and still be identified. In addition, all the sheep are paint-branded on the body for the summer months. The paint brand and ear-tag number correspond. Lost tags can be replaced periodically.

The tags used at one station bear the year of birth, the line of breeding, and individual lamb number. For example, 51-3-1 designates the first lamb born in 1951 in the North Star or 103 line. The 3 is the code number for this line.

The sheep records are kept on individual sheets as shown in Fig. 59. This is really a ewe production record, because it shows the amount of wool and lamb each ewe produces each year. The birth weight, weaning weight, and market score are recorded for each lamb.

Each ewe's production is calculated to a standard hundred-pound-ewe basis. First the lamb weights are adjusted to a 140-day basis. The ewe's wool is then converted to equivalent pounds of lamb. This latter figure is based on a study of Winters (1940) where he found that 1 pound of wool is the equivalent of 3.4 pounds of lamb. He obtained this value from market values of both products over a long period of time.

Production per hundred pounds of ewe is calculated by adding the total lamb produced and adding the lamb equivalent of wool produced. This total production is divided by the ewe's weight and multiplied by 100. The ewe's weight is taken as the average of two weighings on fixed dates.

There is very little selection of females, because a large proportion of the ewe lambs are needed for flock replacements. For this reason, all ewe lambs that are reasonably well grown out and free from obvious defects are saved to help maintain the flock number. The poor producers in the ewe flock are culled on the basis of their production per hundredweight.

The ram lambs are selected largely on the basis of their dam's production per hundredweight. This is where most of the selec-

Year <u>1951</u>							
Original Flock No. _____		Date of Change _____		Ewe No. <u>48-3-8</u>			
Breeding of Ewe <u>North Star (103)</u>							
Matings:							
	Ram	Breed of Ram	Date				
	1. <u>49-3-20</u>	<u>103</u>					
	2. <u>50-3-21</u>	<u>103</u>					
	3. _____						
Lot Breeding	_____						
Ewe Weights:	Nov. 1 <u>137</u>	June 1 <u>125</u>	Average <u>131</u>				
Disposal of Ewe _____							
LAMBING RECORD							
Lamb No.	Sex	Date of Birth	Birth Wt.	20 Weeks Record			Disposal
				Date	Weight	Grade	
<u>51-3-57</u>	<u>F</u>	<u>3/21/51</u>	<u>10.4</u>	<u>7/20/51</u>	<u>58</u>	<u>3</u>	
<u>51-3-58</u>	<u>F</u>	<u>3/21/51</u>	<u>9.0</u>	<u>7/20/51</u>	<u>67</u>	<u>2</u>	
WOOL RECORD							
Date of Shearing <u>4/4/51</u>		Yield of Wool: Grease Wool <u>9.5</u> Scoured Wool _____					
Wool Grades:		(a) Fineness <u>Ch 3/8</u>		(b) Quality <u>good color</u>			
		(c) Length <u>very good staple</u>		(d) Uniformity <u>even grade</u>			
Remarks _____							
Lamb Performance:				<u>51-3-57</u>	<u>51-3-58</u>		
Lamb No. _____				<u>121</u>	<u>121</u>		
Age of lamb at final wt. _____				<u>.39</u>	<u>.48</u>		
Rate of gain (birth to final wt.) _____				<u>65</u>	<u>76</u>		
Weight at 140 days _____							
Total wt. of lamb produced at 140 days <u>141</u>							
Ewe Productivity per 100 lbs.							
Lamb <u>107.63</u>							
Wool <u>7.25</u>				(x 3.4) = <u>24.65</u>			
Total <u>132.28</u>							

FIG. 59. Individual sheep record.

tion is practiced. Every year the ewes' production records are sorted, and the numbers of the top 12 or 15 ewes are listed. The ram lambs from these ewes are saved, and all other ram lambs

are castrated. This eliminates ram lambs from low-producing ewes. When a line becomes well established, and there is a public demand for rams of that line, more ram lambs are left uncastrated.

When the lambs have been weaned and scored, those ram lambs with the fastest growth rate, best fleece, and highest market scores are retained, as possible flock sires. This is individual selection and allows for some flexibility in the system of selection.

In sheep and cattle, where the number of offspring per dam is low, improvement through selection centers more and more on the sires. Selection of ram lambs from the highest-performing ewes allows all the females to be kept, while selection for performance proceeds. This system entails very little record keeping, as the pedigrees are maintained on the female side only. The highest-producing ewes produce the flock sires, and thus insure the multiplication of genes for high production. The whole flock becomes linebred to the best-producing ewes.

This system of selection is practiced in stock where the number of offspring per dam is low. In sheep, the lamb itself forms a large part of the ewe's total production. Exceptional individuals are not likely to be by-passed in selecting on the ewe's total performance. In pigs, where litters are farrowed, any one pig's performance forms only a small part of the dam's total performance, and many exceptional individuals might be overlooked with this system of selection. Similarly, in pigs there are five factors of production as criteria for selection. Exceptional individuals in one or several factors of production can be missed in a system of selection based on a single production figure.

Other records of performance tests have been developed for sheep. Christgau (1938) developed a record of performance for sheep based on weaning weights at about fifteen weeks, postweaning weights at about eight weeks later, lamb grades at the time of the latter weighing, and wool grade and weight. The lambs' rating is really based on postweaning gains. The rams can be rated on the basis of sire differences of postweaning gain of lambs. The ewes are rated on the basis of total performance, which includes both lamb and wool production.

Terrill and Stoehr (1942) found that ewes that weighed heavier as yearlings produced, on the average, more pounds of lamb than lighter ewes. There was no consistent difference in lamb pro-

duction between ewes born as single and ewes born as twins. The importance of selection on body weight before the first breeding was emphasized.

Terrill (1951) reported on the records of inbred Rambouillet lines of sheep from 1938 through 1948. He showed that progress had been made through selection in over-all merit of weanling lambs. The expected progress from selection of sires was far greater than from selection of dams. This substantiates the earlier statement of the sire's special importance in classes of stock where the number of offspring per female is low.

Proved Sires. Reed (1938) reviewed the results of 20 years of proved-sire breeding in Jersey cattle. The use of 8 proved sires in this program had resulted in a marked increase in production over the foundation cows. The average production of the foundation cows was 11,626 pounds of milk and 634 pounds of butterfat. Every sire got daughters whose production averaged well above that of the foundation group. The grand average of 86 daughters of the 8 proved sires was 12,760 pounds of milk and 674 pounds of butterfat, or an increase of 1,134 pounds of milk and 40 pounds of butterfat.

Evidence of progressive benefits of proved-sire breeding is indicated by the fact that daughters topped by only one proved sire averaged 662 pounds of butterfat, those carrying two crosses averaged 682 pounds, and those with three or more crosses averaged 705 pounds. Similar results were reported for Holstein cattle. Sixty-six daughters of proved bulls used in the herd averaged 497 pounds of milk and 49 pounds of butterfat over their dams.

A weakness in many so-called proved sires is that they are not actually proved; too often the proof rests on a highly selected progeny. Unless the test is based on all the offspring (daughters in the case of a dairy bull) or a truly randomized selection, the data may be very misleading. In still other instances the females to which the male is mated are a highly selected group; here the performance of the entire progeny can be very misleading, especially if they are in the hands of an outstanding herdsman.

Most modern dairy indexes make adjustments for the dam's production. The United States Bureau of Dairy Industry compiles a list of proved dairy bulls under the rules of the Dairy

Herd Improvement Association proved-sire program. The following taken from *Agricultural Handbook No. 7, U.S.D.A.* explains very satisfactorily both the method and its use:

Under the rules of this program, all production records of daughters and dams used in the tabulation consist of the first 305 days' production of the lactation period. Records of cows under 6 or over 7 years of age are converted to a 6-year-old basis by using age-conversion factors developed by the Division of Dairy Herd Improvement Investigations, from records of association cows. Records of cows milked three or four times a day during any part of the 305-day lactation period are reduced to a twice-a-day milking basis, by using factors based on the fact that cows milked three times daily or four times daily produce approximately 20 per cent or 35 per cent more milk, respectively, than if they had been milked only twice daily. When more than one lactation record is available, each record is standardized according to the foregoing procedure and the average of all the standardized records is used to represent the producing capacity of the cow.

The information given for each sire may be better understood by studying the following proved-sire record:

	Number	No.	Pounds Milk	Per Cent	Pounds Butter- fat
FOBES RUBY BOY DIXIE 811414 *12	16 daughters	23	15,024	3.4	515
Born, 11-21-40; proved, 3-31-49; alive; Mich.	15 daughters	21	14,928	3.4	513
Sire, 773513; dam, 1770094.	15 dams	36	13,578	3.4	466
Used in Michigan Co-op. A.B.A., Inc.	Difference (11-10-10)		+1,350	0.0	+47

The Holstein sire Fobes Ruby Boy Dixie 811414, as indicated in the second line, was born November 21, 1940, and was proved March 31, 1949. He was alive when proved. In some records a dash (——) follows the date of proving, which indicates that no report was made as to whether or not the sire was alive or dead at the time of proving. The sire was proved with records from Michigan. The third line gives the registration numbers of the sire and dam of the proved sire.

The last line usually lists the owner of the herd in which the sire was proved. In case records from more than one herd were used, the reference is to the owner of the herd from which production records for the largest number of the sire's youngest daughters were reported. If the sire is reported as used in an artificial-breeding association, the name of the association is given in place of the herd owner. This sire was used in the Michigan Co-op. Artificial Breeding Association, Inc.

An asterisk following the registration number of a sire indicates that he appeared in a previous list and that his record has been retabulated

to correct it or to include additional data that have since become available. The figure following the asterisk indicates in which of the 13 previous lists his record appeared. The figure 1 indicates the first list (*Miscellaneous Publication 277*), 2 the second list (*Miscellaneous Publication 315*), and so on. (See footnote 1, p. 1.) In the example above the asterisk and figure 12 (*12) following the registration number indicate that data on the sire appeared in the twelfth list (*Miscellaneous Publication 651*).

Figures at the right show that the sire had 16 daughters with a total of 23 production records averaging 15,024 pounds of milk, testing 3.4 per cent fat, and averaging 515 pounds of butterfat; that 15 of these daughters had 21 production records averaging 14,928 pounds of milk, testing 3.4 per cent fat, and averaging 513 pounds of butterfat; and that the 15 dams of these daughters had 36 production records averaging 13,578 pounds of milk, testing 3.4 per cent fat, and averaging 466 pounds of butterfat. A plus (+) or minus (−) sign indicates whether the average production of the daughters is above or below that of the dams.

The three figures in parentheses (11–10–10) following the word “difference” give a brief comparison of the daughters with their respective dams. The first figure is the number of daughters that equaled or excelled their dams in milk production, the second figure the number of daughters that equaled or excelled in butterfat test, and the third figure the number of daughters that equaled or excelled in butterfat production.

USING THE PROVED-SIRE RECORD

The proved-sire record as summarized in this list should be considered merely as an indication and not as conclusive evidence of the breeding value of the sire in question. In general, however, the greater the number of dam-and-daughter comparisons included in a proved-sire record the more reliable the record as an indication of the breeding value of the sire. Also the greater the number of lactation records included in the average record of each dam and daughter the more dependable the proved-sire record.

If the difference between the average butterfat production of the dams and that of the daughters is less than 25 pounds, the increase or decrease should not be considered as significant. If the daughters of a sire have an average butterfat production of 25 or more pounds above that of their dams the sire may be considered as raising the production of the herd in which he is used. If the daughters' average butterfat

production is 25 pounds or more below that of their dams the sire may be considered as lowering the production of the herd in which he is used, in which case he should be discarded from that particular herd. Such a sire may prove useful in a herd of lower-producing dams, however.

To make the most intelligent selection of a sire, the dairyman should use these proved-sire records to single out the most promising sire and then make every effort to supplement these data with additional information gathered from the herds in which the dams and daughters made their records. Particular attention should be given to the feeding practices and environmental conditions under which the records were made, in order to be assured that the records of the daughters were not made under more favorable conditions than those of the dams or vice versa. It is especially important to determine that there has been no selection of daughters in making the comparison.

A dairyman who wishes more information about a listed sire than is contained in the brief summary may write to the herd owner listed. Or he may address his request to the extension dairyman of the State in which the sire was proved; or, if the sire is reported as used in an artificial-breeding association, he may write to the extension dairyman of the State in which the breeding association is located. He should address his letter as follows: State Extension Dairyman, In Charge of Dairy-Herd-Improvement-Association Work. An address list is given on page 6.

The theory behind the progeny test, sire or dam, is that the young untried individual is selected on the basis of its phenotype, but after it is reselected on the basis of its progeny it is selected on the basis of genotype. Actually genotype plus environment makes phenotype. Purity of genotype is probably seldom compatible with the most desired phenotype, but desirable genes must be present in order to obtain the desired phenotype; hence selections for phenotype if effective must also within limits be effective for genotype.

The above does not have application to dairy cattle or poultry for egg production. In these species the male cannot satisfactorily express his genotype through his phenotype.

Stratton (1952) made a study of the comparative effectiveness of selection in swine before and after testing their progeny. The performance records of the foundation herds of Minnesota No. 1 and No. 2 swine were used as material for the study. The study

was based on dams' records only because the number of sires was so much more limited. Stratton states:

The annual genetic improvement expected to result from the increased accuracy of selection due to the progeny test in the actual herds was generally offset by the increased interval between generations. A comparison of the expected genetic gain due to selection for number of pigs weaned, body score, feed efficiency and growth rate in the theoretical gilt herds and in the actual herds within each line indicated that more annual genetic gain would have been realized in the theoretical gilt herds. The expected annual genetic improvement for litter size was greater in the actual herds than in the theoretical gilt herds. This can be partially explained by the increased intensity of selection for fertility in the actual herds and, thus, a corresponding decrease in the intensity of selection for the other traits considered.

Records of Performance of Beef Cattle. Sheets (1932) proposed a method of measuring the actual performance of beef cattle in efficiency of gain. In this method all the feed consumed by a calf is recorded, including the milk and supplement used during the suckling period. The calves are fed to 900-pounds weight and then carcass-tested. The final record of performance is determined by the number of pounds of cold dressed carcass per hundred pounds of digestible nutrients consumed. Carcass grade and tenderness score are given some importance.

Winters and McMahon (1933) described a method of evaluating performance by the average daily gain from birth to one year of age, and a quality score based on conformation at the end of one year.

Black and Knapp (1936) proposed a method of performance testing for cattle based on efficiency and rate of gain from 500 pounds to 900 pounds. Carcass grade also enters into the final appraisal. This method was found by Black and Knapp (1938) to be a more accurate method of appraisal on the basis of progeny performance than the two other methods described.

In the light of the comparisons mentioned above, Winters (1940) proposed the following procedure for gathering performance data for beef cattle:

1. Record birth weight of calves.
2. Creep feed during the nursing period and wean at a constant weight of 450 pounds.

3. Test the feedlot performance from 500 to 900 pounds.
4. Record the animal's merit in body conformation on a percentage of perfection basis.

Where individual feeding is possible, a record should be kept of feed consumed between 500- and 900-pound weights. The data of carcass appraisals should also be recorded.

Knapp *et al.* (1941) concluded that a program of progeny testing for efficient beef production should be based on rate and efficiency of gain in the feedlot, dressing per cent at slaughter, and carcass grade and uniformity of offspring in these respects.

A program of developing inbred lines of beef cattle is being conducted at the U. S. Range Station, Miles City, Montana. One line of Hereford cattle has been bred and selected for economic performance for 15 years, without the occurrence of a single dwarf calf (Knapp *et al.*, 1951). Improvement in the line for rate of gain was at least 0.16 pound in daily gain and 66 pounds in weight at 15 months of age. This indicates that the methods employed are effective in improving the performance of beef cattle.

The practice followed consists of saving about half of the bull calves in each line and castrating the other half on the basis of the calf's own phenotype and its dam's record (Woodward, 1951).^{*} This first selection is based largely on the milking ability of the dam.

All bull calves are then fed individually on a time-constant test, and the calves are selected on the basis of final weight, average daily gain, and efficiency of gain on feed. If a calf surpasses the record of his sire, he replaces the sire in the breeding herd.

Carcass data are also collected to measure differences between the progeny of various sires.

Females are selected on a weight basis at eighteen months of age.

The system of performance testing just described is very similar to the system practiced for swine and sheep in Minnesota. Selections are based on performance, and no set system of inbreeding is followed. With the low number of offspring and

^{*} Personal communication.

long generation interval in cattle, the accurate testing and selecting of sires becomes the key to the breeding program.

Methods of Selection. Individual, pedigree, and progeny selection are often treated as though they are entirely separate. In practice, the three methods tend to overlap a great deal.

In the preceding pages, a system of selection that is based primarily on individual performance is described. Information on both progeny and pedigree is used as it becomes available. When pedigree selection is used, the information is based on the performance of ancestors. In a performance-testing program, such as described here, the performance of ancestors is available, and some attention is paid to good ancestry. Offspring are not exact replicas of ancestors, however, and individuals are never selected entirely on their ancestry; they must perform well as individuals even when they have good pedigrees.

By inbreeding a herd, the relationship of animals in the herd increases. All the animals then have very similar pedigrees, and there can be almost no pedigree selection. Genetic variation among individuals within the herd becomes reduced; hence the effectiveness of individual selection is reduced.

In progeny selection, the stress is on the performance of the progeny. The drawback is that progeny performance becomes known gradually. Selections often cannot be delayed until the progeny has been tested for such characters as fertility and milking ability. The generation interval is so long in farm animals that in many cases a program of progeny testing takes too long to be practicable. It also requires a large physical plant to carry stock until all progeny information is available. The information for individual selection is available much sooner.

Selection in the Minnesota project is largely on individual performance, but information on performance of progeny is used as it becomes available. For example, boars that sire a uniformly good group of pigs are sometimes used in the herd for several years. These boars are originally selected on their own performance (with some emphasis on pedigree for a character, such as number farrowed, which the boar cannot express directly). They are reselected on the basis of the performance of their progeny. The same procedure is followed for sheep.

Special Types of Selection. Since about 1927 several of what may be labeled special types of selection have been proposed. Actually they are more properly classified under newer systems of breeding and hence are discussed in the final chapter, "Building Superior Germ Plasm." They are convergent improvement, gamete selection, recurrent selection, and reciprocal recurrent selection.

Selection Indexes. Selection indexes are constructed with a view to making maximum improvement in total performance (Lush, 1945). All the characters under selection are combined into one figure. To obtain such an index, the importance and heritability of each trait are required. In addition, the genetic and phenotypic correlations of various traits are needed. All selections are then based on the one figure, which represents total performance.

This would appear to be an almost foolproof method of selection if the information used in constructing the selection index could be known accurately. This information, however, is not known at the time that it is needed. Instead, average values covering a period of time must be used. This difficulty tends to defeat the use of selection indexes in breeding work. Average values of the importance of various traits are not good enough for particular situations. They do not permit the amount of selection for different characters to be varied as their importance to the line or herd varies. As a result, exceptional individuals may be overlooked in selection.

Summary. Selection consists of choosing parents of future generations. It is important that they be chosen as accurately as possible on the basis of performance. The attempt to improve the performance of farm animals through selection is well justified by earlier progress.

A system of selection, based on individual performance, has been outlined. This outline includes the use of progeny and pedigree information as it becomes available.

The characters under selection should be the ones that are most important for high production. The number of characters must be kept low for maximum selection to be practiced. These characters should be accurately measured and standardized.

Inbreeding must be used along with selection. The mating system employed should be a flexible one to allow full use of the available material. The system of selection should also be flexible to permit the greatest amount of selection where there is the greatest need for it.

Judgment should be used along with measurements, but not to replace measurements. A clear objective should be in mind, so that selection can be consistent over a period of years. The foundation animals must be good performers. The numbers used should be large enough to allow rigid selection.

Effectiveness of Selection

Although selection has been practiced from time immemorial, there are few accounts to demonstrate its effectiveness. When the actual performance of a whole herd or flock is improved over a period of years, it is taken to mean that selection has been effective in raising the level of performance. The actual production figures, however, give no indication of how much selection was practiced, or how much improvement was due to better nutrition or management.

If an increase in performance is due to management or some other environmental factor, the performance of the animals will slip back whenever the favorable environment does not prevail. If improvement in performance results from genetic improvement, the change is of a more permanent nature. In order to appraise the effectiveness of selection, more refined methods than mere recording of the performance data are required.

One method at once suggests itself. If a herd is split into two groups, one group can be left without selection, as a control, while selection is practiced in the other group. This method should show the effect of selection. In practice, this method is not so useful. First, it is difficult to get a large enough group of animals that are genetically enough alike at the outset. Second, the experiment stations simply do not have facilities to carry the large numbers of animals for a control and a selected group just to demonstrate the effectiveness of selection. Finally, breeders cannot afford to maintain herds without some selection.

Effectiveness of selection can also be tested by selecting in opposite directions from a common foundation group. This has been done in small animals (Mather, 1949; MacArthur, 1949) and even in swine (Krider *et al.*, 1946; Dickerson and Grimes, 1947). If a low and high line are separated, it is clear that

selection is effective. In farm animals, however, all the interest is in selecting for high performance, and the selection for low lines is wasted effort. An experiment of this nature will not show how much of the selection has been in the plus direction, and how much in the minus direction of performance. The Illinois experiment with swine, although successful in separating two lines, resulted mainly in lowering the performance of the low line. A different method of appraisal must be resorted to.

Selection is generally considered to be effective when it is successful in raising the level of performance of a herd or flock. It is also effective when the level of performance is maintained while the degree of purification is increased. Purification comes about through inbreeding. Greater purification results in a more uniform group of animals in their genetic complex. The *prepotency* of the animals is increased with increased genetic purity. Increased prepotency increases the regularity with which parents transmit their characteristics to their offspring. Prepotency—so desired by animal breeders—is the result of homozygosity or genetic purity and dominance. An understanding of the reason for prepotency should make it clear that selection is effective if it can maintain the level of performance while achieving greater genetic purity. In other words, selection is effective if it can offset the decline that usually accompanies inbreeding.

The difficulties encountered in conducting experiments to measure the effectiveness of selection in farm animals forces animal breeders to a different method of appraisal. This method probably will never be used by the average livestock breeder, but it is useful for experimental herds. It consists of comparing the actual trend of performance over a period of time with the expected trend on the basis of the amount of selection practiced and the heritability of the trait. The effects of inbreeding are also considered.

To make such a comparison valid, the data should cover a sufficient number of years for the good and bad environmental effects to have a chance to cancel each other. If there has been any consistent trend in management, this trend must be measured and accounted for. If the net environmental effects are zero, or near zero, and there has been a change in performance of the herd, it can justly be attributed to selection. This method

of appraisal has been used in the studies of inbred lines. It will now be covered in more detail, and some of the results will be discussed.

TECHNIQUE FOR THE APPRAISAL OF EFFECTIVENESS OF SELECTION

A measure of the *amount* of selection that is practiced is known as the *selection differential*. The selection differential is usually defined (Lush, 1945; Lerner, 1950) as "the average superiority of the selected animals over the average of their generation, weighted by the number of offspring." If an animal leaves no offspring, it has the same effect as if the animal was never selected. It will leave no genes for future generations. Animals that have relatively more offspring will have relatively more opportunity to pass their genes on to future generations, and, therefore, to influence the herd. The weighting should therefore be based on the number of offspring at some definite stage of life. For example, weighting by the number of offspring at birth is not suitable for dealing with such traits as growth rate. A sow that has a litter of ten pigs that die soon after birth will have no more influence on the growth rate of pigs in the herd than a sow that has no offspring.

The definition of a selection differential needs clarification in another respect. In some cases it is more convenient to measure the selection differential as the difference between the average of the selected animals and the average of the *group from which they were selected* rather than the generation from which they were selected. The group from which the animals were selected should be corrected to the same generation basis. This sort of thing occurs where pigs are selected for litter size from both sow and gilt litters. The pigs are selected on the basis of their dam's record. The gilts and sows may be from a different generation, but, when the sow's litter size is adjusted to a gilt basis, it has the effect of putting sow and gilt litters in the same generation. The sows must be given credit for the genetic superiority on which they were selected to place them in the same generation as the gilts. The definition for selection differential is sound, but sometimes groups need to be adjusted to the same generation base.

A simple example of calculating a selection differential follows: Let it be assumed that three gilts *A*, *B*, and *C* are selected from a group of gilts that average 175 pounds at 154 days of age. *A* weighed 190 pounds, *B* weighed 185 pounds, and *C* weighed 200 pounds at 154 days. When these gilts farrowed, they raised 3, 2, and 1 gilts to 154 days of age, respectively. The weighted average of the three selected gilts is:

$$\begin{array}{r} 3 \times 190 = 570 \\ 2 \times 185 = 370 \\ 1 \times 200 = 200 \\ \hline 6 \qquad 1,140 \end{array}$$

1,140 divided by 6 equals 190 pounds.

The selection differential for these gilts is:

Average of selected gilts: 190 pounds

Average of all gilts in the group: 175 pounds

The gilt selection differential is 15 pounds for 154-day weights.

This is a measure of the superiority of the selected gilts. The superiority of the selected males can be similarly calculated. The two figures can be combined into one selection differential for this generation. This is an estimate of the *amount* of selection that is practiced for 154-day weight per generation. The selection differentials for the other traits are similarly computed.

An increase of 15 pounds per pig at 154 days in the next generation is not to be expected. Some of the 15 pounds superiority of the selected gilts is due to environmental causes. Some of the superiority will probably be due to favorable interactions of the particular genes of these gilts. Because of segregation and recombination, the offspring of these gilts will not have exactly the same genes as the gilts and consequently will not have the same gene interactions. How much superiority can be justly expected in the offspring of these gilts? If the heritability of 154-day weight is 20 per cent, 20 per cent of the 15 pounds or 3 pounds superiority in the offspring of these gilts with respect to 154-day weight is the maximum that can be expected.

It was previously stated that heritability was a ratio of the additively genetic variation over the total variation of a trait. It is therefore clear that, the higher the heritability of a trait,

the more accurate is the selection. A heritability of 20 per cent is the same as identifying a genotype with a 20 per cent degree of accuracy.

If it is desired to know how much progress can be expected per year from the selection practiced, it is necessary to change the 3 pounds per generation to a per year basis. To do this, we must know the generation interval of the herd. The generation interval is defined as "the average age of the parents when their offspring are born" (Lush, 1945). This age is again weighted by the number of offspring of each set of parents. The method of weighting will vary with the investigator, but let us weight the age of the parents by the number of *daughters that farrowed*. This is a figure that has a direct bearing on future generations. Table XII is an example to aid in clarifying the calculation of generation interval.

TABLE XII. THE CALCULATION OF GENERATION INTERVAL

	Age of Dam, Months	Age of Sire, Months	Average Age of Parents, Months	No. of Daughters That Farrowed	Weighted Age of Parents, Months
Litter 1	24	12	18.0	3	54.0
Litter 2	19	12	15.5	2	31.0
Litter 3	24	12	18.0	3	54.0
Litter 4	13	12	12.5	1	12.5
Litter 5	26	12	19.0	2	38.0
				<hr/>	<hr/>
Total				11	189.5
Average					17.2

The average generation interval of these pigs is 17.2 months, which equals 1.43 years.

The gain expected per year for the example becomes 3 pounds divided by 1.43 or 2.1 pounds per year.

The improvement of 2.1 pounds at 154 days of age needs at least one further correction. It is possible, by statistical techniques, to determine how much decline results in 154-day weight with each per cent increase in inbreeding. Let us assume that the inbreeding in the herd rose from a coefficient of inbreeding of zero to one of 30 per cent over a 10-year period. This is equivalent to a 3 per cent increase in inbreeding per year. Fine (1951)

found that 154-day weight decreases 0.658 pound for each per cent increase in inbreeding. The inbreeding in our example results in a decline of 3 times 0.658 or 1.97 pounds at 154 days. The net effect of selection in this particular example amounts to 2.1 minus 1.97 or a 0.13-pound increase in 154-day weights per year. This is called the annual expected genetic gain. It is the result of selecting pigs that weigh 15 pounds heavier than the average of their generation, when due allowance is made for heritability, generation interval, and effect of inbreeding.

The expected genetic gain per year can be expressed as the *amount* of selection (selection differential) times the *accuracy* of selection (heritability), divided by the generation interval. From this amount is subtracted the annual decline from inbreeding. Symbolically, this can be represented as follows (Fine, 1951):

$$m = \left(\frac{sH}{G} \right) + bI$$

where m = the expected genetic change per year.

s = the selection differential.

H = the heritability of the trait.

G = the generation interval.

b = the effect of inbreeding (for each per cent).

I = the average increase in inbreeding per year.

In our example this is:

$$m = \left(\frac{15 \times 0.20}{1.43} \right) - (3 \times 0.658) = 2.1 - 1.97 = 0.13 \text{ pound}$$

If we now obtain a regression coefficient of the average annual 154-day weights on time, we can compare it with our expected gain. This regression coefficient is really a measure of the trend of the actual performance of our pigs with respect to 154-day weights. If the 154-day weights have increased over the 10 years of our experiment, the regression coefficient will have a plus sign; if the 154-day weights have decreased, the sign of the regression will be minus.

For convenience, let it be assumed that in the above example the agreement between the expected and the actual gain was very good. What does this mean? It means, first of all, that the

actual gain was as much as could be reasonably expected on the basis of the selection practiced. It means, further, that through selection it was possible to maintain the performance of the pigs with respect to 154-day weights and, at the same time, increase the genetic purity of the pigs from no inbreeding to an average inbreeding coefficient of 30 per cent. Selection would indeed be effective if this could be accomplished in the short period of 10 years.

An average annual gain of 0.13 pound in weight at 154 days would probably not be perceptible. Furthermore, the various figures that go into the computations of the expected genetic gain are subject to much error. Methods such as the one described are nevertheless very useful in appraising the effectiveness of selection in a general way. A small but consistent gain in performance for each of the characters under selection can amount to considerable improvement over a period of years. This is particularly true if the gain is accompanied by genetic purification.

As stated in the previous chapter, correlation of traits under selection can affect the accuracy of selection. If two desirable traits are positively correlated, selection for one will aid in selection for the other. Where a desirable character is positively correlated with a non-desirable one, selection will be more difficult. Exact phenotypic and genetic correlations of various traits for a number of herds will help in determining how much relative selection to practice for each trait. Some of the present correlations will probably be changed in the process of molding new lines. Those correlations due to pleiotropy and similar effects will always complicate the selection process.

In some cases, it may be that certain superficial traits are correlated with factors of production. If such correlations are recognized, they will be of great help in selection. This is actually what breeders imply when they select for type in order to improve production. Unfortunately many of the characters that are used to evaluate type really have no association with performance.

Evaluation of Results. The inbred lines at Minnesota have reached a fairly high degree of inbreeding. The increase in the coefficient of inbreeding from zero to about 40 per cent implies a great deal of genetic purification. A study by Fausch (1953) of the relationship between inbreeding and variability in per-

formance of the Minnesota No. 1 swine showed a general tendency for increased rather than decreased variability. The tendency is illustrated in Table XIII with the data on weaning weight and this is typical of birth weight, 154-day weight and fertility.

TABLE XIII. THE RELATIONSHIP BETWEEN INBREEDING AND VARIABILITY IN WEANING WEIGHT IN THE FOUNDATION HERD OF MINNESOTA No. 1 BREED OF SWINE

Inbreeding Groups	Number of Litters	Number of Pigs	Total Variance	Total Coef. of Variance	Within Litter Variance	Within Litter of Coef. Variance
0-9	16	135	63	23	32	16
10-19	52	424	80	27	31	17
20-29	101	894	69	26	41	20
30-39	125	1,105	82	29	49	22
40-49	17	162	93	27	61	23

The crossbred progeny with the Minnesota No. 1 as one of the parental stocks showed a decrease in variability (England, 1953). The indications therefore are that inbreeding brought about a decrease in genetic variance but an increased variance in phenotype because of the inbreds' greater susceptibility to environmental changes.

R.O.P. The Inbred Livestock Registry Association has a system of Record of Performance testing in swine. In this scheme, the animals on test are rated by starrng on the basis of performance. Fertility, growth rate, feed efficiency, and type are all considered in the evaluation of the performance of tested pigs. A minimum performance is essential to obtain a one-star rating. The highest rating is a five-star classification.

If this system is effective in making selections, the higher-starred animals should produce more starred animals than no-star or low-star parents. Furthermore, the higher-starred animals should contribute more to the later generations of the herd. Blackburn (1951) conducted a study along this line on Minnesota No. 1 data. He found that the pigs with higher star ratings produced more offspring that rated stars, and, also, made a greater contribution to the future generations of the herd. The high-producing animals perpetuated their high production in future generations.

TABLE XIV. CONTRIBUTIONS TO THE 1951 BREEDING HERD BY TYPE OF MATING

Type of Mating	3-Star or Higher × 3-Star or Higher	Star × Star	Star × No Star	No Star × No Star
	3-Star or Higher	Star	No Star	No Star
1939-1949				
Number of matings	169	255	272	69
Number of contributions	47	60	60	11
Contributions per 100 matings	27.8	23.5	22.1	15.9
1944-1949				
Number of matings	102	158	176	47
Number of contributions	31	41	39	3
Contributions per 100 matings	30.4	25.9	22.2	7.0

Some of Blackburn's results are shown in Table XIV.

The relative contribution of the high-starred matings to future generations is higher than that for low-star or no-star matings. This emphasizes the importance of record of performance testing.

APPRAISAL OF SELECTION IN DIFFERENT HERDS

Inbred Lines from Crossbred Foundations. Fine (1951) studied the data of the Minnesota No. 1 and Minnesota No. 2 swine to determine how well the amount of selection agrees with the performance of these lines when due attention is given to heritability, length of generation, and effect of inbreeding. Both of these lines were started from crossbred foundations. The Minnesota No. 1 was developed from a Tamworth-Landrace cross; the Minnesota No. 2 from a Poland China-Yorkshire cross.

The average amount of selection that was practiced in both males and females is shown in Table XV.

The expected genetic gain for each trait, along with the actual change per year, is shown in Table XVI.

From this study, Fine concluded that the expected and actual genetic change in the various traits agreed fairly well. He concluded further that selection was an important factor in the development of the Minnesota No. 1 and the Minnesota No. 2 swine.

TABLE XV. AVERAGE ANNUAL SELECTION DIFFERENTIALS FOR MINNESOTA No. 1 AND MINNESOTA No. 2 HOGS

	Minnesota No. 1	Minnesota No. 2
Number of pigs born alive	0.73 pigs	0.48 pigs
Number of pigs weaned	0.81 pigs	1.14 pigs
Body score	0.61 points	0.22 points
154-day weight	15.1 pounds	10.2 pounds
Rate of gain	0.13 pounds	0.06 pounds
Economy of feed	-8.1 pounds	-0.6 pounds

TABLE XVI. ACTUAL AND EXPECTED GAIN IN MINNESOTA No. 1 AND MINNESOTA No. 2 HOGS

	Number Born	Number Weaned	Body Score, Points	154-Day Weight, Pounds	Rate of Gain, Pounds	Economy of Gain, Pounds
Minnesota No. 1						
Expected	-0.041	-0.291	+0.086	-0.335	+0.005	3.13
Actual	-0.037	-0.260	+0.017	-1.278	-0.012	1.92
Minnesota No. 2						
Expected	-0.058	-0.208	+0.079	-2.824	-0.029	0.59
Actual	-0.183	-0.155	+0.177	+0.826	+0.004	-0.51

Outbred Herds. Damon (1951) analyzed the records of two outbred herds of swine maintained by the Hormel Institute at Austin, Minnesota. These swine consisted of a Duroc herd and a Chester White herd. The data included only the farrowing and weaning records. The size of the selection differentials for the number of pigs farrowed and weaned are shown in Table XVII.

TABLE XVII. AVERAGE SELECTION DIFFERENTIALS FOR NUMBER OF PIGS FARROWED AND WEANED

	Chester White	Duroc
Number of pigs born alive	1.72	3.31
Number of pigs weaned	1.56	3.00
Weaning weight per pig, pounds	3.03	0.70

The nature of the data made it possible for Damon to demonstrate and measure a consistent upward trend in management for the years during which the data were gathered. In his data the plus and minus environmental affects did not cancel each other. Damon was able to correct for the upward trend in management in his calculations on expected genetic gain.

With the same data, Damon was able to show that considerable automatic selection was taking place for size of litter at birth and at weaning. He defines automatic selection as "the amount of selection that would occur automatically if the number of pigs selected from each litter is proportional to the number of pigs available in each litter."

The actual and automatic selection differentials for number farrowed and number weaned are presented in Table XVIII.

TABLE XVIII. ACTUAL AND AUTOMATIC SELECTION DIFFERENTIALS

	Chester White		Duroc	
	Actual	Automatic	Actual	Automatic
Number farrowed	1.72	1.00	1.56	1.15
Number weaned	3.31	1.94	3.00	1.93

When the automatic selection differentials are subtracted from the actual differentials, how much conscious selection was practiced for these traits is shown.

The expected and actual changes for number of live pigs farrowed and the average litter weaning weight from Damon's data are presented in Table XIX. The number of pigs weaned was strongly influenced by a disease problem in these herds, and these data are not included here.

TABLE XIX. EXPECTED AND ACTUAL CHANGES IN OUTBRED HERDS

Characteristic	Breed	Expected Change	Actual Change
Number of live pigs farrowed	CW	0.062	0.089
Number of live pigs farrowed	D-J	0.081	0.063
Average litter weaning weight	CW	0.141	0.206
Average litter weaning weight	D-J	0.104	0.176

Damon concluded that "selection played a vital rôle in effecting noticeable increases on two of the three measures of sow productivity considered in his study."

Inbred Lines within a Breed. Rempel (1952) analyzed the data from 8 inbred lines of Poland China swine, developed at Minnesota. These lines were developed along with the Minnesota No. 1 and Minnesota No. 2. Actually, 13 lines of Poland China were started in 1937. Some of these lines were culled

early, and dropped from the program. Some of the remaining lines were combined into a new line. There were no introductions from the outside into any of these lines. All the foundation animals were outbred Poland China swine. The form of the analysis was similar to the one described earlier.

The average annual amount of selection that was practiced is shown in Table XX.

TABLE XX. AVERAGE ANNUAL SELECTION DIFFERENTIALS IN INBRED POLAND CHINA LINES

	Number Born	Number Weaned	Body Score	154-Day Weight	Rate of Gain	Economy of Gain
V	+0.88	+0.99	+0.70	+17.50	+0.14	-2.2
B.S. (Morris)	+0.33	+0.48	+0.70	+19.83	+0.16
W.L.	+0.89	+1.01	+0.78	+19.43	+0.21
A	+0.90	+0.56	+0.58	+14.73	+0.11	-3.13
B.S. (Crookston)	+1.11	+1.38	+20.65	+0.14
M.L.	+0.77	+1.16	+18.40	+0.14
B	+1.15	+2.33	-2.35	-0.02
C	+1.17	+1.66	+17.63	+0.14

The average annual expected and actual gains are presented in Table XXI.

The actual and expected changes in performance for these inbred lines is in fairly close agreement for all characteristics considered, except 154-day weights. This trait shows a slight, but consistent, negative expected change. Actually the lines showed a small but consistent positive change. The reason for this apparent discrepancy is a too severe allowance for the effect of inbreeding on 154-day weights. When this is taken into account, the data show that the actual gain achieved corresponds with that which should be expected on the basis of the amount of selection practiced.

The last three studies mentioned all show that selection is effective in maintaining performance. It is important to note that in both the lines from crossbred foundations and the lines from within a breed, the genetic gain corresponded to the amount of selection practiced.

The size of the selection differentials in the outbred herds was relatively large for several reasons. With no inbreeding, the amount of variability in these herds should be greater. Secondly, the number of pigs in these outbred herds was much larger than in any one of the inbred lines. The gain achieved in out-

TABLE XXI. AVERAGE ANNUAL GENETIC CHANGES IN PERFORMANCE OF INBRED POLAND CHINA LINES OF SWINE

Line	Number Born		Number Weaned		Body Score		154-Day Weight		Rate of Gain		Economy of Gain	
	Expected	Actual	Expected	Actual	Expected	Actual	Expected	Actual	Expected	Actual	Expected	Actual
V	-0.035	-0.014	-0.293	-0.030	+0.080	+0.011	-0.115	+0.041	+0.010	+0.001	+1.191	+0.184
B.S. (WC)	-0.145	+0.010	-0.555	+0.016	+0.088	+0.028	-0.672	+0.562	+0.010	+0.005
W.L.	-0.089	+0.010	-0.462	-0.014	+0.080	+0.032	-0.837	+0.306	+0.015	+0.003
A	-0.019	-0.008	-0.303	-0.001	+0.069	+0.016	-0.210	+0.485	+0.007	+0.005	+2.085	-0.025
B.S. (NW)	-0.060	-0.063	-0.429	-0.064	-0.705	+0.136	+0.007	+0.004
M.L.	+0.078	-0.071	-0.405	-0.054	-0.367	-0.00004	+0.010	+0.002
B	-0.010	+0.052	-0.104	+0.063	-2.446	-1.095	-0.012	-0.008
C	+0.091	-0.002	+0.113	+0.006	+1.586	+0.213	-0.019	+0.003

bred herds will, however, be more easily dissipated than that made in inbred lines. The gain achieved in inbred lines is achieved along with purification, and is, therefore, of a more stable nature.

The level of performance in all the inbred lines studied at Minnesota has been fairly well maintained. This level of performance is much higher, however, for those lines that were started from crossbred foundations. It appears that high-performing inbred lines can be more readily obtained by starting from a crossbred foundation than by starting lines within a breed. Inbred lines will transmit their performing ability with more regularity than outbred stock. In outbred stock, the gains from selection will be lost very rapidly, once selection is relaxed. This is true for inbred lines as well, but to a lesser degree, as a result of the homozygosity achieved from inbreeding.

The preceding remarks are based on results with swine. The general principles apply equally well to other classes of stock. It should be borne in mind, however, that the effectiveness of selection will be relatively less for classes of stock that produce relatively fewer young. The length of generation will also affect progress from selection. The exact methods to employ will vary with the class of livestock.

Summary. Breeders cannot afford to keep livestock without selection, or with selection for low performance, just to test the effectiveness of selection. The effectiveness of selection can be evaluated, however, by comparing the gain expected on the basis of the amount of selection (with due regard to heritability, generation interval, and effect of inbreeding) with the actual trend of performance over a period of time. The time must be a sufficient number of years to allow year-to-year differences to cancel each other.

The studies of selection presented show that the actual and expected changes are in close agreement for the herds studied. The studies show that selection is an effective agent in the development of inbred lines within a breed, and in lines from a crossbred foundation. Selection is also effective in bringing about changes in outbred stock, but the changes are probably of a less permanent nature than those in inbred lines.

Results have been presented to show that the performance of inbred lines has been fairly well maintained while a great deal

of purification has been achieved. The purification is manifested by a reduction in variability.

The analysis of R.O.P. data shows that the higher-rated animals, on the performance basis, produce more high-performing offspring, and contribute more to future generations than the animals with a lower performance rating.

CHAPTER XIII

Inbreeding

Inbreeding may be defined as the mating of individuals more closely related than the average of their breed or the population concerned. It is clear, therefore, that inbreeding may vary greatly in intensity—from the mating of individuals that are only slightly related to the mating of those as closely related as sire and daughter or full brother and full sister. In contrast outbreeding is the mating of individuals less closely related than the average of their breed or the population concerned.

It is unsatisfactory to define inbreeding as the mating of related individuals because all animals that can be mated have some common relationship. The degree of relationship for inbreeding may vary greatly. The degree of relationship depends upon the number of genes possessed in common by the two animals that are mated. It is likely that in the mating of a mare to a jack the number of genes common to the two parents is not large, comparatively speaking. The number of genes common to both parents may be expected to increase progressively, from the mare-jack mating, in the following types of matings: Clydesdale to Belgian, Clydesdale to Clydesdale, two Clydesdales belonging to the same family, and finally two Clydesdales that are brother and sister. The expected genetic width between matings is given below with the closest at the top.

Self-fertilization

Full brother and sister or parent and offspring

Half brother and sister, uncle and niece or nephew and aunt

Half uncle and niece or nephew and half aunt

First cousins

Random mating within a line *

Random mating within a breed *

Outbreeding within a breed

Crossing of definite families within a breed

A cross of breeds

A cross of inbred lines of different breeds

A cross of species

A cross of genera

* This type of mating could be much closer than indicated.

At the time of fertilization each of the genes contributed by the dam is paired with a gene from the sire. The members of a given gene pair may be alike, so that the individual is pure or homozygous for that gene pair, or they may be unlike so that the individual is impure or heterozygous for that gene pair. This situation is extended to the many gene pairs involved. Every mating is therefore fundamentally a mixture of the essentials of both inbreeding and crossbreeding, because gene pairings at the time of fertilization include genes that are alike and genes that are unlike.

The mating of related individuals increases the pairing of like genes. The closer the mating and the more often the inbreeding is continued in successive generations, the higher will be the degree of genetic purity attained.

General Effects of Inbreeding. Since inbreeding by promoting the pairing of similar genes increases the likelihood that the new individual will inherit similar traits from its two parents, genetic purity is promoted. Naturally, the closer the mating and the longer the practice is continued in successive generations, the greater will be the degree of purification.

Since inbreeding increases the likelihood of similar genes becoming paired, it reduces the percentage of heterozygosis. Inbreeding necessarily promotes the segregation of types, especially during the first one or two generations after a cross. The principle is illustrated simply by the dihybrid ratio: a cross of $AAbb \times aaBB$ in the F_2 generation yields the phenotypic ratio $9AB$ to $3Ab$ to $3aB$ to $1ab$. Ab and aB are parental types; AB and ab are new types brought out by the segregation. In practice many gene loci with their accompanying allelomorphic series are involved. An individual can possess only two genes and a gamete one gene of any particular series. If a given breed possesses the allelomorphic series A, A^1, A^2, A^3, A^4 , an individual belonging to the breed can possess only two of the genes; let us assume they are AA^1 . When this individual produces germ cells either A or A^1 is put into each of the germ cells. Let us assume that the AA^1 individual is a male and sires many offspring. When his offspring are interbred the chances that any one individual will receive two A 's or two A^1 's is greatly increased, and thus the entire population of descendants will receive more A and A^1 genes than is common to the breed as a

whole. Inbreeding therefore automatically decreases the number of genes of any and all allelomorphic series that become incorporated in the inbred strain or family. By the above process the percentage of homozygotic genes is automatically increased.

Increased genetic purification has the automatic effect of generally bringing about an over-all reduction in vigor. The explanation for this rests in the causes of hybrid vigor (Chapter XIV); inbreeding may be called crossbreeding in reverse. As crossbreeding has the general effect of stimulating vigor, so inbreeding naturally has the opposite effect. Inbreeding automatically induces purification for both the more desirable and the less desirable genes. Because of the complications of linkage in many instances some of the more desirable and the less desirable genes are closely linked. Such linkage in itself, even with rigorous selection, is sufficient to cause a general reduction in vigor. It is accentuated by loss of the factors responsible for hybrid vigor, such as dominance and, in some cases, gene interaction.

Practical breeders have often been disappointed with inbreeding because they seldom obtain as desirable animals from the practice as from outbreeding. The point often missed is that, although it is highly desirable to have inbred lines as desirable in phenotype as possible, inbreds should be appraised primarily by genotype. Inbreeding is a tool to be used primarily for the building of desirable genotypes, whereas crossbreeding is of special use in the building of desirable phenotypes. (Under certain conditions crossbreeding may also be used to build more desirable genotypes.) In the years ahead livestock breeders are going to appreciate more and more the difference between genotype and phenotype.

Reasons for Inbreeding. The three basic reasons for inbreeding are:

1. To promote genetic purity and thereby increase prepotency.
2. To bring undesirable recessives to light and give the breeder the opportunity of culling them from the stock.
3. To promote the sorting of highly heterogeneous genetic materials into various gene complexes, which will thereby allow for more effective selection for desirable gene complexes.

The closebred animal is expected to be the prepotent one, because it is more nearly homozygous. The animal that pos-

sesses the higher degree of homozygosity by necessity produces germ cells more uniform in genetic constitution. It is possible that a closebred animal may be homozygous for a large number of recessive characters. If such an animal is mated to an individual possessed of a large number of dominant characters, for which it may be rather heterozygous, the latter individual will appear as prepotent as, or even more prepotent than, the former. This, however, cannot usually be expected to occur, because in general it is believed that the more desirable characters are stimulated by dominant genes, and, if the inbreeding is accompanied by a rigorous program of selection, it is likely that more dominant than recessive genes will have been made homozygous.

Prepotency is a valuable asset to an individual, a line, and a breed. Inbreeding helps to build prepotency. In livestock breeding inbreeding has not been used extensively in the past for the development of prepotency, but we may expect that it will be used much more for that purpose in the future.

The first and foremost reason for inbreeding is the purification of the bloodlines. Continued inbreeding when supplemented by rigid selection is the quickest and surest method of fixing and perpetuating a desirable character or group of characters. During recent years inbreeding has been used to develop definite inbred lines which are more nearly homozygous than existing lines, with the expectation that some of the lines will cross to advantage. It is also hoped that the inbred lines will be sufficiently purified to produce a consistent amount of advantage from crossing. This approach may be considered an experiment to find a definite method by which inbreeding can be used in constructive animal breeding. It is essentially a copy, with some modifications, of the method that has been used with so much success in corn breeding.

Some of the old breeders used inbreeding for the very purposes given above. Bakewell, the Colling brothers, and Bates, among others, used inbreeding for purposes of purification before the science of genetics was known. They had no means of knowing that inbreeding induced a higher degree of homozygosis, but by experience they learned that inbreeding increased the purity of the stock so produced.

Other breeders have practiced inbreeding (usually not close) with the perpetuating of the breeding of a certain individual as

the objective. By this type of mating an attempt was made to retain a high degree of relationship to a certain outstanding individual. This type of breeding is illustrated in Fig. 60. By this type of mating the degree of relationship retained is usually not especially large. It will not build a high degree of homozygosity, but it may materially change the gene frequency. It has the general effect of holding variation in check since no violent outcross is introduced.

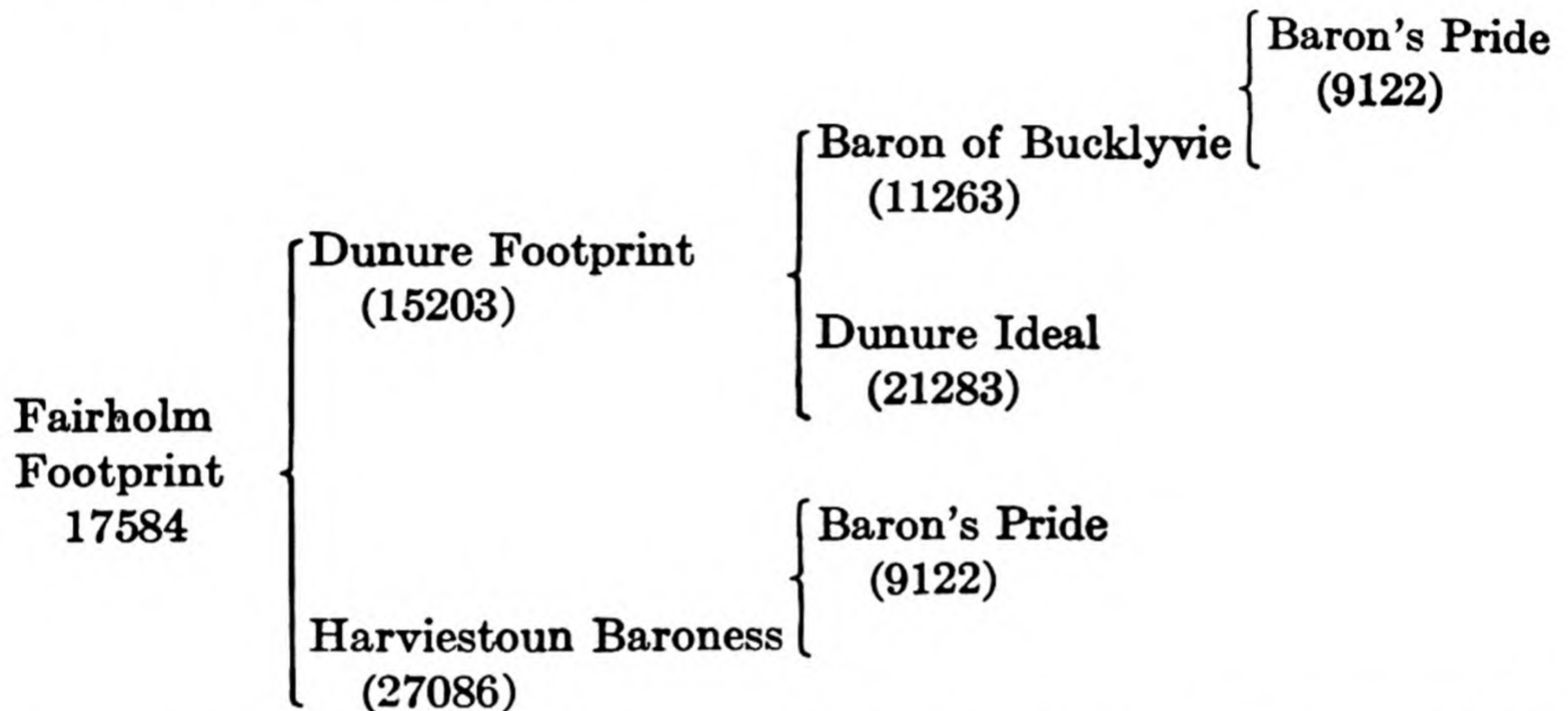


FIG. 60. The pedigree of Fairholm Footprint 17584, an illustration of inbreeding in practice.

Another reason that led some breeders to inbreeding was that in the development of certain breeds it has happened that some breeder was so far advanced over other breeders that for him to go outside for breeding animals would have been a step backward. Cruickshank and Gudgeon and Simpson are reputed to have practiced inbreeding for this reason rather than because they believed in inbreeding as a tool in animal improvement.

Inbreeding and its accompanying promotion of genetic purity automatically bring undesirable recessive genes into view. The breeder is then offered the opportunity of culling these genes from his breeding stock. Culling of the individuals that exhibit the character produced as a result of the homozygous state for the recessive gene or genes is not sufficient to make any major contribution to livestock improvement. It is the parents of such individuals that must be culled. These are the individuals carrying the undesirable gene in a heterozygous condition; hence, the genes pass unrecognized except through a breeding test.

There can be no question but that some improvement can be made in livestock by ridding the breeds of undesirable recessives. It does not appear, however, that this will prove as effective as was once generally assumed. On the basis of what is now known regarding genic interaction, it is entirely possible that some genes that by themselves in a homozygous state produce less desirable results than other genes in a homozygous state may be extremely useful when in a heterozygous condition. However, some very undesirable characteristics arise from the homozygous state of one or two pairs of genes. The elimination of genes of this type from a herd or breed would certainly be of material advantage. Lethals and sub-lethals are discussed in Chapter IX. It is not likely that all lethals could be eliminated by the simple process of inbreeding and culling individuals that possess the undesirable gene in both the homozygous and heterozygous state. It is entirely possible that some lethal and sub-lethal conditions are the result of gene interaction. Nevertheless, it is quite clear that a great deal of improvement could be made by a thorough cleansing of our stocks of many undesirable genes. Inbreeding is a means of promoting this process.

Not much has been stated or written about the third reason given above for inbreeding, to promote the sorting of genetic material into various gene complexes, namely, planned or artificially induced segregation. In the author's opinion, this may well prove to be a major benefit from inbreeding. This is an advantage of special significance when the breeder starts from a rather highly heterozygous population.

Inbreeding automatically reduces the size of the various allelomorphic series included in the original population to be inbred, and, at the same time, particularly if the inbreeding is somewhat mild, it promotes the grouping of the different genetic materials into varied gene complexes. On the basis of what is becoming known regarding gene interaction, it appears that more attention needs to be given to gene complex action than has been done in the past. Regardless of whether the breeder realizes it or not, the selection of individuals for his breeding herd always results in the selection of gene complexes. In view of what is becoming known today, regarding balanced heterozygous states, and the fact that natural selection favors the heterozygote, it appears

possible that inbred lines of livestock which possess only a relatively low degree of inbreeding may prove more useful to the livestock industry than the more highly purified lines. It is entirely possible that a relatively low degree of inbreeding (30 to 40 per cent) when accompanied by a rigorous system of selection may give sufficient purity to allow enough uniformity of both phenotype and genotype for practical purposes. At the same time inbreeding may actually aid in the development of enough balanced heterozygosity to be helpful in the maintenance of the line or family being developed.

Regardless of the above proposed possibility, there is no question but that inbreeding from a heterozygous base does promote the regrouping of genetic materials. The regrouping results in breaking up old gene complexes and the development of new gene groupings. This, in turn, offers the breeder the opportunity of more effective selection.

Kinds of Inbreeding. Actually there is only one kind of inbreeding, but it may vary widely in the degree of intensity. In practice, however, livestock breeders frequently differentiate between inbreeding and linebreeding. By linebreeding the breeder has in mind the mating of animals not closely related, for example, the mating of cousins or of grandparent and grandoffspring. The livestock breeder usually linebreeds in order to retain a higher degree of relationship to a certain individual. By so doing he is attempting to hedge on the future. In the end, however, so-called linebreeding is merely a mild form of inbreeding, and all inbreeding is of necessity linebreeding. Inbreeding automatically reduces the number of ancestors, but it cannot change the number of ancestral places; thus, as a certain ancestor comes to fill several ancestral places, the descendants are linebred to this ancestor.

Linebreeding also varies in its degree of intensity. The pedigree of Beau Blanchard (Fig. 61), which was the result of using a half nephew, Beau Mischief, on his half aunt, Blanche 23d, is a good illustration of linebreeding. Six of Beau Blanchard's eight great-grandsires either are or trace to Anxiety 4th. If continuous outcrossing had been followed, Beau Blanchard would on the average have retained only about a 3 per cent relationship to Anxiety 4th. By the method of linebreeding followed, Beau

Blanchard retained a relationship to Anxiety 4th of about 25 per cent. He was about as closely related to Anxiety 4th as a grandson, even though he was four, five, and six generations removed.

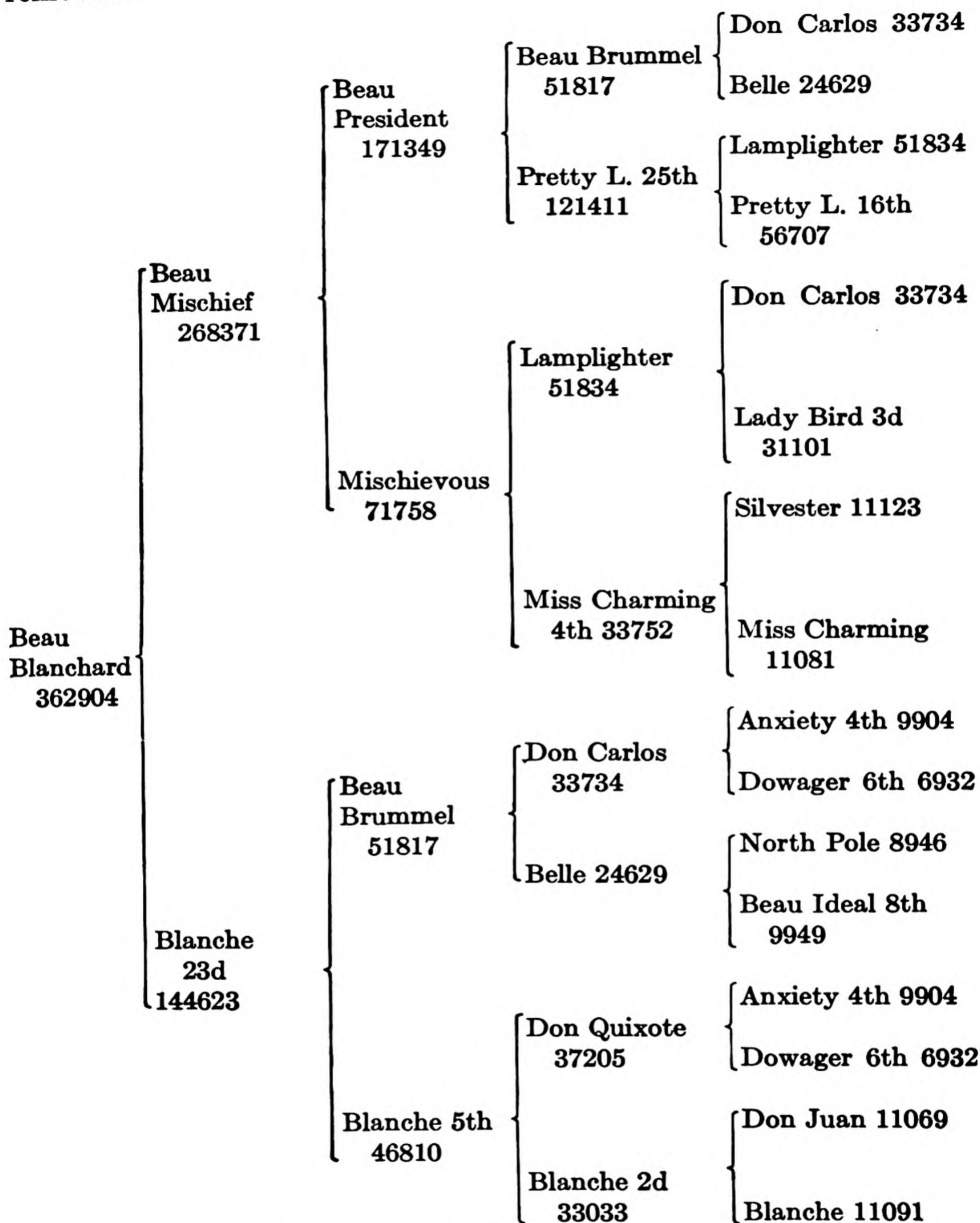


FIG. 61. Pedigree of Beau Blanchard 362904, an illustration of close linebreeding.

The actual amount of purification achieved by the inbreeding of Beau Blanchard probably was not great because he carried a coefficient of inbreeding of only about 11 per cent. As a result of the inbreeding practiced the heterozygosity was decreased about 11 per cent.

The pedigree of Prince Rupert 29th (Fig. 62) is a type that is usually called linebreeding, although the amount of inbreeding is very slight. Linebreeding no closer than this has practically no effect on the homozygosity of the stock.

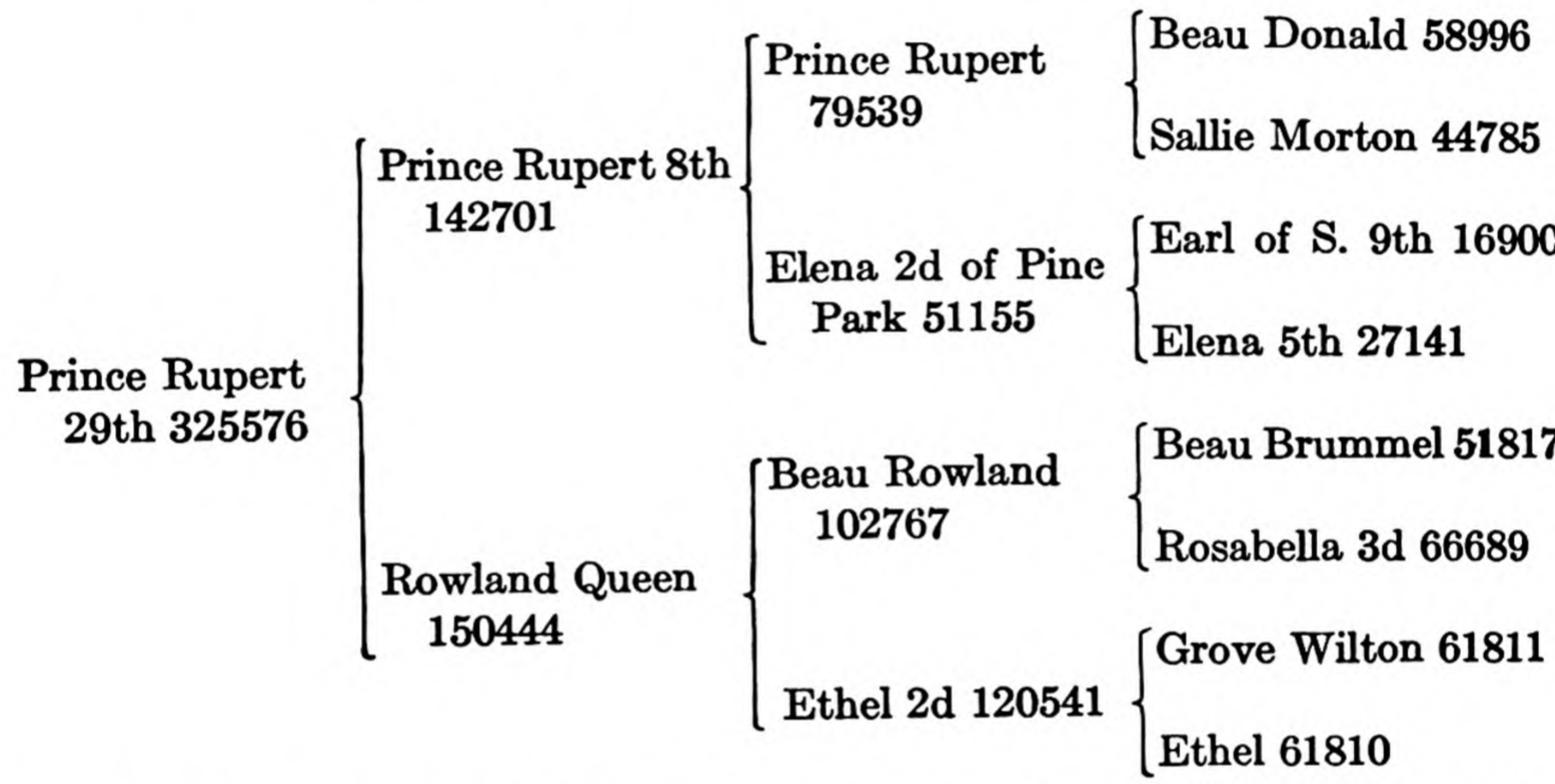


FIG. 62. Pedigree of Prince Rupert 29th, an illustration of diffuse linebreeding.

The accompanying illustrations show that in practice linebreeding takes on various forms. It can readily be seen that these would result from the matings of cousins, half cousins, half uncle and niece, granddaughter and grandsire, double grandsons and granddams, and so on. If any real distinction is to be made between linebreeding and inbreeding it can be made best on the basis of objective. As a rule the breeder who, as he says, “linebreeds but does not inbreed,” is attempting to retain a higher relationship to a certain individual or individuals than would result from outcrossing.

By inbreeding the breeder usually implies a close mating, such as the mating of full brother and sister, parent and offspring, or half brother and sister. A difficulty in distinguishing between linebreeding and inbreeding on the basis of degree of closeness is in deciding the proper point of division. Another difficulty is

that if the distinction is made and linebreeding is continued persistently it may eventually cross the borderline in degree of closeness and become inbreeding.

Since linebreeding is of necessity inbreeding and inbreeding is of necessity linebreeding they should be thought of as one process, namely, inbreeding which varies in its degree of intensity.

The Measure of Inbreeding. Both breeders and scientists have made various attempts to measure the intensity of inbreeding produced by different systems of matings. The result has been that various formulae have been put forward, none of which, however, was an accurate measure until Wright gave us his coefficient of inbreeding. As stated by Wright (1922), "An inbreeding coefficient to be of most value should measure as directly as possible the effects to be expected on the average from the system of mating in the given pedigree." The effects of inbreeding are the fixation of characters and increased prepotency; these are in direct proportion to the percentage of homozygosis; the percentage of homozygosis is in direct proportion to the degree of inbreeding. Thus calculating the percentage of homozygosis that on the average will follow from a given system of mating gives the most natural coefficient of inbreeding.

On the assumption that we are starting with a random-bred stock that is 50 per cent heterozygous, Fig. 63 illustrates the decrease in heterozygosis in successive generations of inbreeding according to various systems of mating. Although Fig. 63 was obtained by theoretical analysis, it coincides nicely with Wright's experimental results, as measured by the decline in vigor, from inbreeding a random-bred stock of guinea pigs.

The coefficient of inbreeding is the expected departure from the heterozygosity prevailing at the onset of the inbreeding.

The sire and dam of the inbred individual have a common ancestor or ancestors. The summation of the coefficients for every line by which the parents are connected gives the coefficient of inbreeding of the individual in question. Each line is traced back from the sire to a common ancestor and then forward to the dam. It passes through no individual more than once, but the same ancestors may occur in more than one line.

In a textbook of this kind the reader is interested in the application of the coefficient of inbreeding rather than the mathematical deductions by which it is derived. He should, however,

bear in mind that the formula was arrived at by consideration of the percentage of departure from the number of homozygous factors in the random-bred stock in the direction of complete homozygosis.

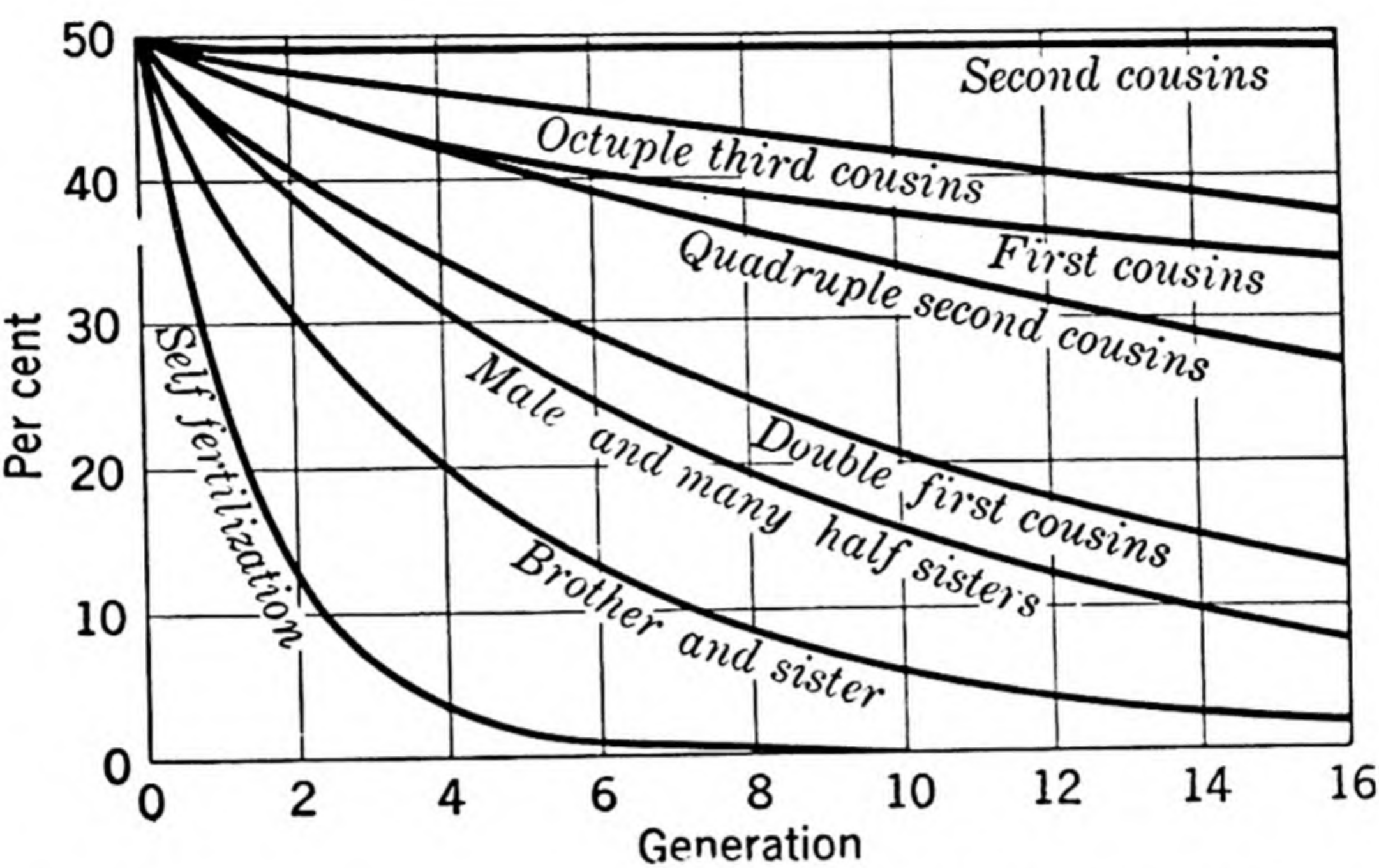


FIG. 63. The decrease in heterozygosis in successive generations of inbreeding according to various systems of mating. (After Wright, U.S.D.A. Bulletin 1121.)

The formula for obtaining the coefficient of inbreeding is

$$F_x = \Sigma[(\frac{1}{2})^{n+n'+1}(1 + F_A)]$$

in which F_x and F_A are the coefficients for the individual and the common ancestor, respectively, and n and n' are the number of generations between the common ancestor and the sire and dam, respectively.

The formula may now be applied (Table XXII) to the pedigree of Roan Gauntlet (Fig. 64). Roan Gauntlet traces twice to

TABLE XXII. DERIVING THE COEFFICIENT OF INBREEDING OF ROAN GAUNTLET, 45276

(After Wright, *American Naturalist*)

Individual	Common Ancestors of Sire and Dam	F_A	n	n'	$(\frac{1}{2})^{n+n'+1}(1 + F_A)$
Roan Gauntlet 45276 (35284)	Champion of England	0	2	1	0.062500
	(17526)		2		0.062500
	Lord Ragland (13244)	0	3	3	0.007812
			3		0.007813
					<hr/> 0.140625

Champion of England through his sire and once through his dam. He also traces twice through his sire and once through his dam to Lord Raglan. For illustration, it is assumed that Champion

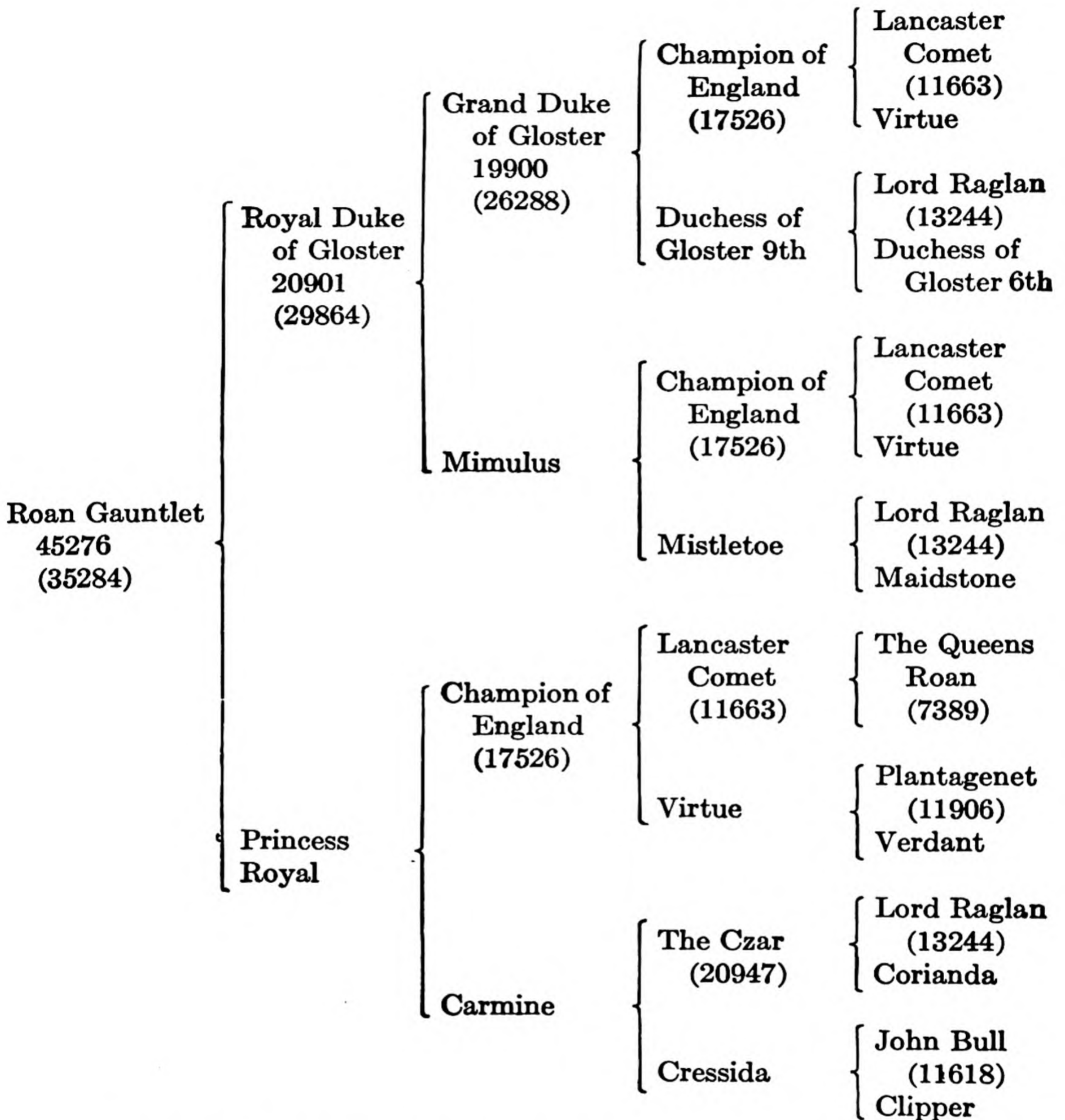


FIG. 64. The pedigree of the Shorthorn bull, Roan Gauntlet.

of England and Lord Raglan are not inbred nor related to one another. F_x , the coefficient for the individual, is therefore 0 in the case of Champion of England. The sire, Royal Duke of Gloster, is two generations removed from Champion of England on his sire's side. and the dam, Princess Royal, is only one gen-

eration removed; n and n' are therefore 2 and 1, respectively. The formula is expanded as follows:

$$\begin{aligned} \left(\frac{1}{2}\right)^{n+n'+1}(1 + F_a) &= \\ \left(\frac{1}{2}\right)^{2+1+1}(1 + 0) &= \\ \left(\frac{1}{2}\right)^4(1) &= 0.0625 \end{aligned}$$

Royal Duke of Gloster is also two generations removed from Champion of England through his dam; hence there is a second tie, due to Champion of England, between the pedigrees of the sire and dam. The inbreeding due to Lord Raglan is worked out

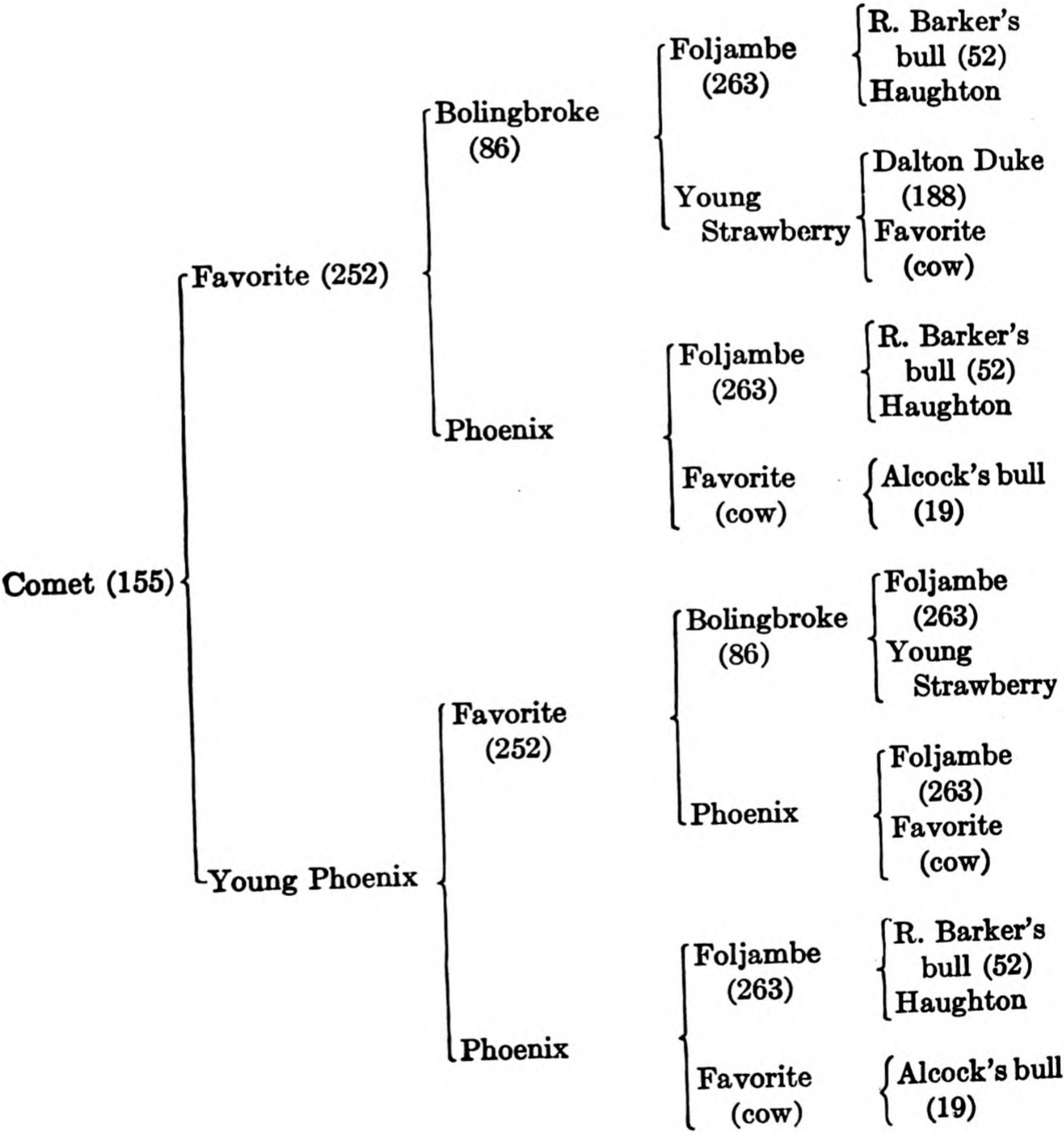


FIG. 65. The pedigree of the Shorthorn bull, Comet.

in like manner. The total is added; in this case it is 0.140625, and it represents the coefficient of inbreeding of Roan Gauntlet.

The pedigree of Comet furnishes an illustration of closer inbreeding (Fig. 65). His sire, Favorite, was also inbred; hence the coefficient of inbreeding for Favorite must first be worked out. By the application of the same formula and as already explained, the coefficients of inbreeding of both Comet and his sire Favorite are arrived at as shown in Table XXIII.

TABLE XXIII. DERIVING THE COEFFICIENT OF INBREEDING OF THE SHORTHORN BULL, COMET (115)

(After Wright, *American Naturalist*)

Individual	Common Ancestors of Sire and Dam	F_A	n	n'	$(\frac{1}{2})^{n+n'+1}(1 + F_A)$
Favorite (252)	Foljambe (263)	0	1	1	0.1250
	Favorite (cow)	0	2	1	0.0625
					<hr/> 0.1875
Comet (115)	Favorite (252)	0.1875	0	1	0.2969
	Phoenix	0	1	1	0.1250
	Foljambe	0	2	2	0.0312
	Favorite (cow)	0	3	2	0.0156
					<hr/> 0.4687

The coefficient of inbreeding for Comet is much higher than that obtained for Roan Gauntlet. In this case the pedigree of Comet is extended to only the fourth generation; if it is carried to the beginning of the herdbook, the coefficient of inbreeding for Favorite becomes 0.192 rather than 0.188. In general, remote common ancestors have little effect on the coefficient of inbreeding.

The Measure of Relationship. A measure of relationship is valuable because through it we may obtain an index of the degree of relationship that exists between two individuals or between a group of individuals. The two individuals may have the same coefficient of inbreeding but not be related. The formula for arriving at the coefficient of relationship of two individuals is:

$$R_{xy} = \frac{\Sigma[(\frac{1}{2})^{n+n'}(1 + F_A)]}{\sqrt{(1 + F_x)(1 + F_y)}}$$

In this case *A* represents a common ancestor; *x* and *y* the two individuals whose relationship we wish to measure; *n* and *n'* the number of generations the individuals by which *x* and *y*, respectively, are removed from the common ancestor; and *F_A*, *F_x*, and *F_y* the coefficients of inbreeding of *A*, *x*, and *y*, respectively.

The formula for arriving at the coefficient of relationship between the sire and dam of the individual *x* is:

$$R_{SD} = \frac{2F_x}{\sqrt{(1 + F_S)(1 + F_D)}}$$

If full brother and sister are mated, by substitution the formula becomes:

$$R_{SD} = \frac{2(25 \text{ per cent})}{\sqrt{(1 + 0)(1 + 0)}} = \frac{0.50}{\sqrt{1}} = 50 \text{ per cent}$$

TABLE XXIV. THE COEFFICIENTS OF INBREEDING AND RELATIONSHIP OBTAINED FROM DIFFERENT SYSTEMS OF MATING

(From data by Wright, *Journal of Heredity*)

Type of Mating	<i>F_x</i> , Per Cent	<i>R_{SD}</i> , Per Cent	<i>R_{xA}</i> , Per Cent
Nephew and aunt (half)	6.25	12.5	36.4
Half brother and sister	12.5	25.0	47.1
Full brother and sister	25.0	50.0	44.7
Two generations of full brother and sister	37.5	60.0	42.7
Three generations of full brother and sister	50.0	72.7	40.8

F_x represents the coefficient of inbreeding of the individual.

R_{SD} represents the relationship between sire and dam.

R_{xA} represents the relationship between the individual and one of the common ancestors, grandsire, great-grandsire, etc., to which the inbreeding is due.

Application of the Coefficients. Neither of the coefficients is absolute, but they are relative measures. In inbreeding, the coefficient measures the probable similarity of the germ cells

which united to produce the individual; and in relationship, it measures the probable similarity of the genetic constitutions of the two individuals.

The particular use of these coefficients is for the study of breeds and lines within a breed. By them the student can analyze and compare individuals, groups, and breeds for the part inbreeding has played in their respective developments. It also gives some idea of the degree of homozygosity to be expected.

Teachers of animal breeding and breed history may give their students many useful exercises working out coefficients of inbreeding and relationship. As a rule one finds that the animal in question is not nearly so highly inbred as is generally thought.

Calculating Coefficients by the Approximate Method. To write the complete pedigree and work out the full coefficient of inbreeding for a group of individuals of the older breeds is a long and tedious task. Wright and McPhee (1925) developed an approximate method by which much of the detail is avoided. The method is quite accurate for a large group but valueless for individuals. The method involves use of two-column pedigrees. The sire and dam are both recorded, and each of their ancestral lines are run back in single pedigree lines. The choice of sire or dam, in each case, is determined by coin tossing; if heads turn up the sire is taken, and if tails the dam.

To calculate the coefficient of a two-pedigree sample, it is necessary to note only that there is a tie; the number of generations to the closest common ancestor need not be counted. The coefficient then becomes either 50 per cent or 0, according to whether a tie does or does not occur. The two-sample pedigree determination of the coefficient of inbreeding for the individual means practically nothing, but for a group it is nearly as accurate as the more detailed method. For example, if 100 two-column pedigrees are tabulated in which 50 show a tie and 50 do not, the average inbreeding for the group becomes 50×0.50 or 0.25 per cent.

The probable error is calculated by the formula

$$E_p = 0.6745 \sqrt{\frac{pq}{N}}$$

where N = the number of cases, p = the observed chance occurrence of a tie, and $q = (1 - p)$, the chance of non-occurrence. In the case given

$$E_p = 0.6745 \sqrt{\frac{0.50 \times 0.50}{100}} = 0.0337$$

But, since 50 per cent of the ties correspond to an inbreeding coefficient of 25 per cent, the probable error must be rated down, proportionately; it becomes 1.685 per cent.

As already noted, the above shortened method is of little value in determining the coefficient of inbreeding for a particular individual. It may, however, be used with a reasonable expectation of accuracy if the pedigree is tabulated for five generations and if each of the 32 lines is followed to the foundation stock by the random method already given. In this instance, since there are 16 random lines back of both the sire and the dam, there are 256 tabulated pairs of lines to be considered for possible ties. The contribution assigned to a tie in the random part of the pedigree for a pedigree which is complete for k generations beyond the parents is $(\frac{1}{2})^{2k+1}(1 + F_A)$. If k is 4, as recommended, the formula becomes $(\frac{1}{2})^{(2)(4)+1}(1 + F_A)$.

If the tie occurs between the complete portion of the pedigree on one side and the random portion on the other, the formula $(\frac{1}{2})^{n+k+1}(1 + F_A)$ is used. Where the tie occurs in the complete portion of the pedigree on both sides, the usual formula $(\frac{1}{2})^{n+n'+1}(1 + F_A)$ is used.

The coefficient of relationship is also calculated readily by the shortened method. A tie between single random lines back of the two animals in question, X and Y , gives a coefficient of

$$\frac{1 + F_A}{\sqrt{(1 + F_x)(1 + F_y)}}$$

A tie between two-column pedigrees contributes

$$\frac{1}{2} \left[\frac{1 + F_A}{(1 + F_x)(1 + F_y)} \right]$$

to the coefficient; in like manner a tie in four-column pedigrees contributes $\frac{1}{4}$.

The shortened methods eliminate much detailed work. The degree of accuracy has been checked by Wright and McPhee; the coefficient of inbreeding of the 64 Bates Duchess Shorthorns is 40.9 per cent from the complete pedigrees and 42.2 per cent from the random samples of four-column pedigrees.

The Practice of Inbreeding. In general it may be said that inbreeding has a rather poor reputation. Apparently it has long been in ill repute, if we may judge from the writings of Aristotle.

It has been reported that the Arabs inbred their horses very extensively. If we are to accept Ridgeway's opinions regarding the Arab's art and knowledge of animal breeding, we must conclude that the Arab inbred his horses because of indolence and lethargy rather than because of comprehension; and we must further conclude that few or no bad results accompanied the practice, because he happened to possess a very pure and high-grade strain of horses. However, no attempt to answer it will be made here; possibly no entirely satisfactory answer ever will be made.

Regarding the general practice of inbreeding it is known that the earlier breeders practiced inbreeding to a much greater extent than it is practiced today. Robert Bakewell in the eighteenth century demonstrated that inbreeding could be used effectively to improve livestock. Practically every breed of livestock was founded, and the type fixed, by some closebreeding.

The early Shorthorn breeders, the Colling brothers, Thomas Bates, and the Booths, all practiced closebreeding very extensively. The pedigree (Fig. 65) of the bull Comet (155), which at public auction sold for \$5,000, the record price up to that time, is a good illustration of the continued inbreeding frequently practiced by Charles Colling. Even Amos Cruickshank, who for twenty-five years had combed the British Isles for suitable bulls, was finally forced to inbreed; he used one of his own products, Champion of England (17526) by Lancaster Comet (4663). It is generally held by those most familiar with his work that he would have realized his ambitions earlier had he resorted sooner to the use of his own bulls. At first Cruickshank was cautious about inbreeding, but, once satisfied that he was on the right track, he did not deviate from the new path. He was very careful, however, in his selection, regarding both in-

dividuality and ancestry. A good example of his free breeding back to the Champion of England is furnished in the pedigree of Roan Gauntlet (35284) (Fig. 64), which proved to be the most famous of his later-day stock bulls.

Many of the early Hereford breeders, and especially John Price, practiced inbreeding, as did the early Shorthorn men. Gudgell and Simpson, the great American improvers of Herefords, were, like Cruickshank, forced to inbreed. Before resorting to inbreeding and the free use of bulls bred by themselves—

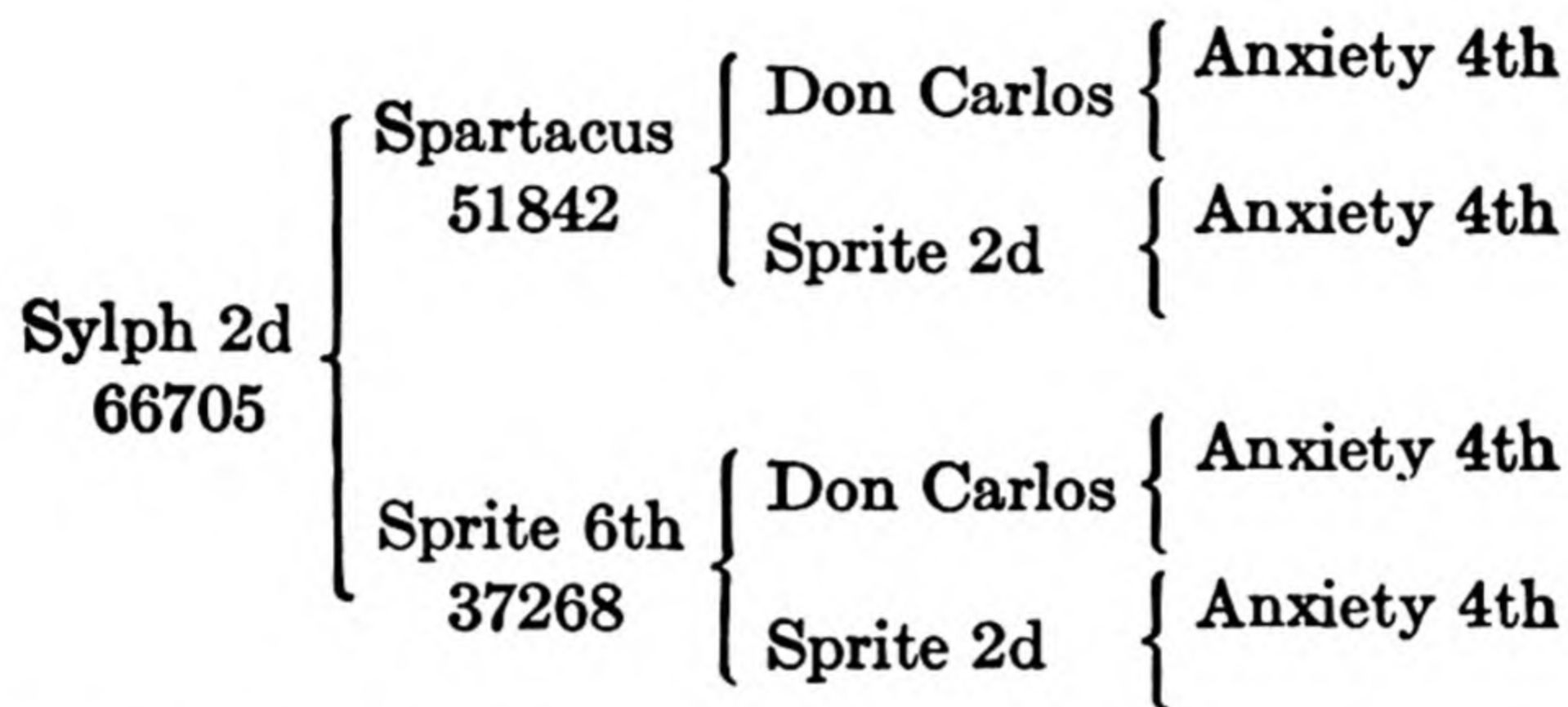


FIG. 66. The pedigree of Sylph 2nd 66705, an illustration of inbreeding as practiced by Gudgell and Simpson.

sons and grandsons of Anxiety 4th—they made many futile attempts to introduce new blood by the use of bulls from other herds, and finally they resorted to getting new blood from outcrosses through the dams rather than through the sires. A very good example of the closebreeding finally resorted to—concentrating the blood of Anxiety 4th—is furnished in the pedigree of Sylph 2d 66705 (Fig. 66). This cow had only one grandfather and one great-grandfather.

Robert H. Hazlett established at Eldorado, Kansas, one of the great beef herds of history. This herd was bred as a closed herd for about thirty years. The size of the herd was large; hence the coefficient of inbreeding for the herd was low although a few individuals were rather highly inbred.

In the early development of the Aberdeen-Angus breed, closebreeding also was freely practiced. For a time, many Aberdeen-Angus breeders linebred to females, following the plan of using an Erica bull only on an Erica female (Erica was the foundress of a famous Aberdeen-Angus tribe) or a Blackbird bull on a Blackbird female. Linebreeding to females is followed with far

more difficulty than linebreeding to males, because, as a female cannot produce nearly so many offspring as a male, selection is made difficult.

The author has observed that the outstanding Aberdeen-Angus herds in Scotland were bred by a comparatively mild form of inbreeding. Though perhaps by coincidence, the three herds that he considered the most outstanding were bred by the same method. Each of the three herds, it so happened, used three herd bulls, and according to the information given by the herd owners, it was their policy to use two bulls, bred in their own herds, the third bull being a purchased bull, but one that was a close descendant of stock sold from their own herd. This plan, therefore, allowed for the introduction of a small amount of outside genetic material. The inbreeding within the herd was not close but close enough to maintain a high degree of genetic stability in each of the herds so bred. At the same time, the method allows for the introduction of some outside genes.

The author found that Scotch breeders of Hill sheep made use of inbreeding in a somewhat similar manner to that mentioned above as used by the Scotch Aberdeen-Angus breeders. Sheep breeders, however, did not buy any sires from the outside. They occasionally purchased females in order to introduce some outside breeding into their essentially closed flocks. The system would have the same genetic effect as that mentioned above for the leading breeders of Aberdeen-Angus cattle, namely, the maintenance of a high degree of genetic stability. However, the introduction of occasional genetic material makes genetic improvement possible (see page 383 for a discussion of gamete selection).

Sheep breeders have not, on the whole, practiced closebreeding; but McKerrow Farms of Pewaukee, Wisconsin, for several years, closebred their Shropshires to Imp. Bibby's 133. A good illustration of the type of closebreeding practiced by them is furnished in the pedigree (Fig. 67) of Senator Bibby Type 499886. The veteran Berkshire breeder, A. J. Lovejoy, of Roscoe, Illinois, was an advocate of closebreeding; the following extract from a statement made by him to Davenport is of interest in this regard.

There is no sire of any breed so prepotent as an inbred sire. When we get to the point where we feel the need of outside blood, we mate an imported sow with our best boar, and from this litter we select a

boar to use on the get of his own sire from other sows in the herds; that is, we breed this boar on his own half-sisters.

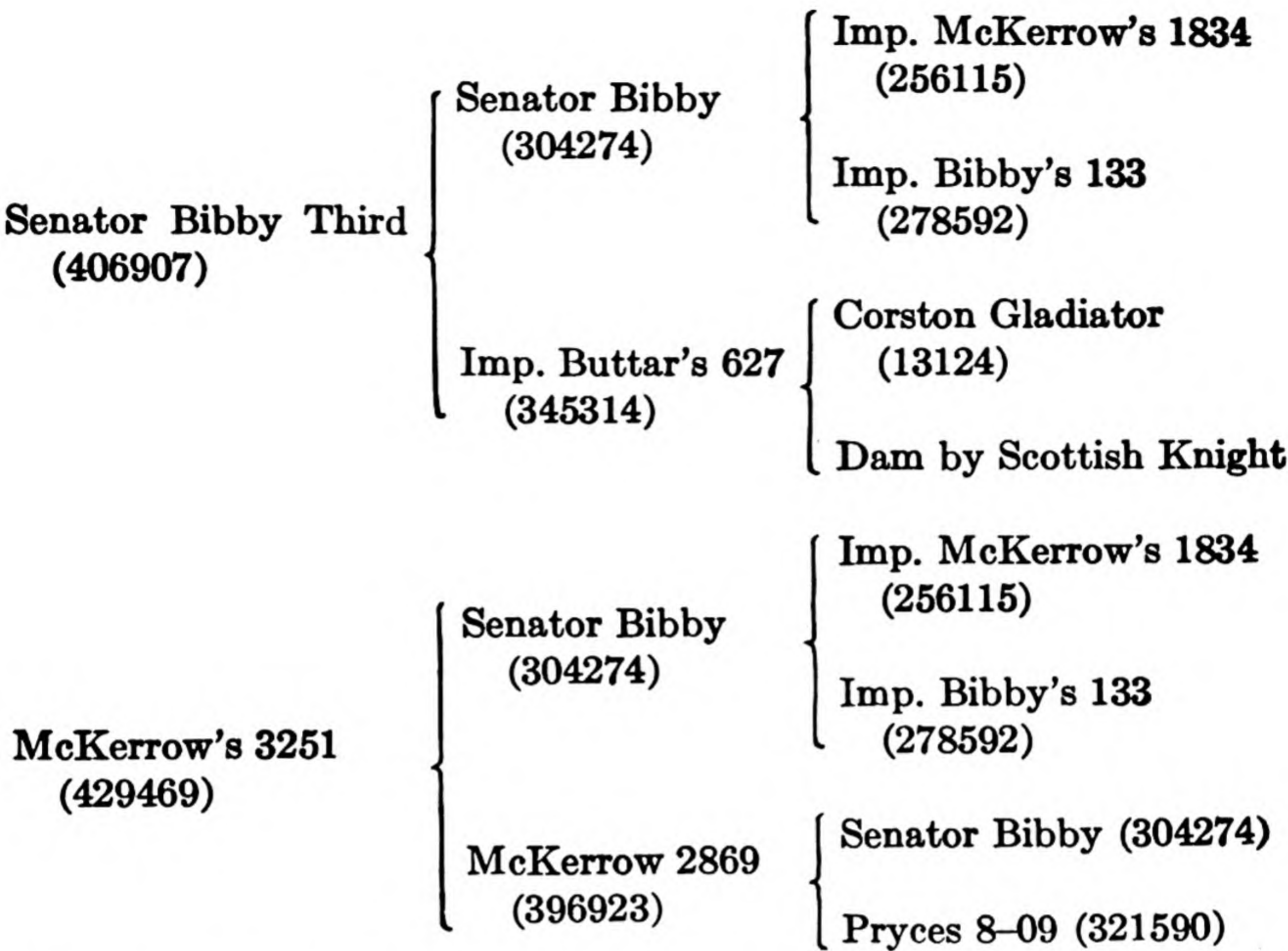


FIG. 67. The pedigree of Senator Bibby Type 499886, an illustration of closebreeding as practiced by McKerron Farms.

Experimental Inbreeding. Bos inbred rats for six generations, with the result that the average size of litter for the first three was 7.5 whereas that for the last three was only 3.2. Weismann inbred a family of rats for twenty-nine generations and obtained a decline in litter size of 6.1 for the first ten generations to 4.2 for the last nine. Darwin, Van Guita, Ritzema-Bos, and Crampe also each concluded that degeneration accompanied inbreeding.

Since these early experimental results coincided so nicely with the popular opinion that inbreeding was deleterious in its effects, the question was for a number of years considered settled. Not content with the answer, Castle *et al.* (1906) inbred *Drosophila* for fifty-nine generations, and no diminution in either vigor or fecundity was encountered. In some instances a slight reduction was obtained, but, when parents from more vigorous strains were chosen, this was avoided. An interesting point is that, when two of the closely inbred strains were crossed, individuals superior

in productiveness to either of the inbred parental strains were produced.

King's Inbred Rats. A most significant experiment on this subject was planned and executed by Miss Helen King (1918 and 1919) of the Wistar Institute. The foundation stock consisted of a litter of four albino rats, two females and two males. One female called *A* was bred to one litter brother, and the other sister, called *B*, was bred to the other litter brother. Brother-to-sister matings were continued for twenty-five generations, the descendants of the *A* female being known as the *A* series and the descendants of the *B* female, the *B* series.

Breeding stock from the *A* series was selected from the litters having the largest number of males, and from *B* series from litters having the largest number of females. The result was that the *A* series possessed a sex ratio of 122.3 males to 100 females, and the *B* series had a sex ratio of 81.8 males to 100 females. Inbreeding in itself, however, had no effect on the sex ratio, for inbreeding for six generations without selection did not alter the sex ratio. Actually selection took advantage of the segregation which was occurring. These results led to King's belief that there is a very delicate chemotactic reaction between ova and sperm, and that the male is of little importance in sex determination.

The selection practiced by King was rigorous. From the data given we may infer that after the sixth generation only about 1 out of 12.5 females produced was retained for breeding purposes.

Inbred males belonging to the seventh to fifteenth generations, inclusive, were heavier at all ages than stock albinos; in the adult stage they were about 18 per cent heavier than the general run of stock albino males and 12 per cent heavier than the selected stock series, reared under the same environment. The inbred females were only slightly heavier than the stock females; in the adult stage they were 3.7 per cent heavier. The inbred rats of both sexes from the sixteenth to the twenty-fifth generations were superior in weight to the stock rats of the same period.

The inbred males were more variable in weight than stock males up to 60 days, and inbred females showed more variability in weight than stock females up to 90 days; after these ages the stock rats showed slightly more variability. An important point is that the variability in weight decreased at the rate of about

2 per cent for three generations of inbreeding up to the fifteenth generation. Segregation for body weight was occurring, and by selection the stock was being purified for weight.

Fertility was increased while the inbreeding was practiced, the stock series having an average litter size of 6.7 and the inbreds, 7.5. King found that high fecundity, early sexual maturity, and vigorous growth are characters which are inherited as a group. In other words, by selecting for vigorous growth, early sexual maturity and high fecundity were also obtained. Since all three are physiological activities, seemingly dependent upon general well-being, it is natural that there should be a high correlation among the three. If similar correlations hold true for farm animals this is of much practical importance.

Furthermore no impaired constitutional vigor resulted from the inbreeding, and the inbreds lived longer. These two characters likewise are dependent upon general body strength and well-being.

The inbred males were less active, more timid and nervous, and somewhat more savage than the stock males. This is not attributable to the inbreeding but to the fact that no selection was made to eliminate these traits, which are probably, as pointed out by King, heritable behavior complexes. It is also plausible that they are closely interwoven.

We may infer that at times, at least, the bad results experienced by livestock breeders from inbreeding are due to failure to guard against certain weaknesses. The breeder who is intent on fixing type is likely to overlook the less conspicuous characters, such as fertility, longevity, and even growth rate.

Inbred Guinea Pigs. Another important inbreeding experiment was the inbreeding of guinea pigs by Wright (1922). Twenty-three separate families were developed by brother-to-sister matings; over 25,000 animals were recorded in the inbreeding experiment; over 4,000 were recorded in the control stock, in which inbreeding was carefully avoided; and nearly 500 were recorded in crosses between the different inbred lines. In some of the families inbreeding was carried out for twenty generations.

Marked differences between the twenty-three inbred families were brought out. Certain subfamilies also became differentiated. On the average there was a decline in all the elements of

vigor studied as compared with the random-bred stock. When, however, crosses were made between the inbred lines a marked improvement over both parental stocks was obtained. Apparently nothing desirable was lost by the weeding-out process of inbreeding, but the full benefits of crossbreeding were realized only when the crossbreds themselves became parents.

When the crossbreds were subjected to inbreeding a decline in vigor was again experienced which was proportional to the decrease in heterozygosis.

An important point brought out by this experiment is that there appeared to be no heredity of general vigor; there was no correlation between the success of families in raising their young and weight, size, or frequency of litters. Weight was not correlated with regularity in producing litters; there was no correlation between the percentage born alive and the percentage raised or between average size of litter and litter frequency. These results are somewhat at variance with the results obtained by King in which high fecundity, early sexual maturity, and vigorous growth were inherited as a group. However, they need not necessarily agree, for if, in a certain species, breed, or strain, desirable factors are closely linked with undesirable factors the effects of inbreeding will be very different from those which will be experienced if no such linkage is present. It is also highly probable that so complicated a character as general vigor is due to the combined effects of many factors. Hence we cannot expect the detailed results from one inbreeding experiment to coincide with those of another.

Experimental Inbreeding of Farm Animals. King's and Wright's published results were soon followed by several experiments in inbreeding farm animals. The development of hybrid corn probably furnished a greater stimulus to the inbreeding of farm animals than the studies of inbreeding in laboratory animals.

The United States Bureau of Animal Industry (1937) started six inbred lines of Poland China swine, six of Tamworth, and several of Chester White. Full brother \times full sister matings were made. Several lines were lost in the early generations of inbreeding, and others were lost later or were discarded because of poor results. Two Chester White lines were carried to the seventh generation. In general, the inbreeding was accompanied

by a loss of vigor. There was a decline in the number of pigs farrowed and raised, the rate of growth decreased, and the feed required to produce a unit of gain increased.

Hughes (1933) began inbreeding Berkshire swine in 1922 and reported that the inbreeding was not accompanied by any noticeable loss of size or vigor. He reported a coefficient of inbreeding of 0.74 for the herd. The inbred group as a whole averaged more pigs per litter (9.78) than the outbred Berkshire herd (8.14). Hughes reported some decrease in the size of litters among the inbreds as the inbreeding continued. No noticeable color change or structural abnormality was brought out by the inbreeding. Hughes states: "The results obtained thus far seem to agree in part with those of Miss King (no noticeable loss in size or vigor) and in part with the results of other workers (there has been a slight decrease in size of the inbred litters)."

Godbey and Starky (1932) also inbred Berkshires and reported that the inbreeding did not appear to affect birth weight but that weaning weight appeared to be reduced.

Willham and Craft (1939) reported on a study of inbreeding and outbreeding Duroc swine. Matings approximating half brother \times half sister were made for eight generations. The inbred stock was inferior to the outbred stock in number of pigs born alive, birth weight, number of pigs weaned, daily gains, feed per unit of gain, the coefficient of digestibility, and haemoglobin level.

Lush and Culbertson (1937) reported on the effects of inbreeding Poland China swine; the herd was closed to outside breeding, and four boars were used each year. The project was initiated in 1930 and the report made in 1937. The pigs farrowed in 1937 had an average coefficient of inbreeding of 15.4 per cent. They reported that the more highly inbred pigs tended to be smaller at weaning and gained more slowly than the pigs with less inbreeding. These observations of reduced vigor are now being confirmed as the general and expected results of increased genetic purification. In the modern development of inbred lines an attempt is made to offset these general effects through increased efforts in selection for performance.

Hodgson (1935) developed three highly inbred lines of Poland China swine by full brother \times full sister matings. Hodgson reported difficulties in obtaining matings between litter mates: the

number of pigs born alive was less among the inbreds than among the outbreds, and the losses after birth were much heavier among the inbreds than among the outbreds. The inbreds required more time to reach 200 pounds in weight. On the other hand, Hodgson reported that some of the highly inbred individuals performed very satisfactorily. Two of the above-mentioned lines were later culled to make room for the development of new lines, but the third one has been retained. This line, known as the Minnesota M line, was increased in numbers and carries a coefficient of inbreeding of about 85 per cent. It appears unlikely that the line will prove useful to commercial swine production. They cross well, but their own performance is far too low.

Woodward and Graves (1933) reported results on inbreeding grade Guernsey and grade Holstein-Friesian cattle that are very interesting and encouraging regarding what can be done with inbreeding in livestock improvement. The inbreeding of the Holsteins was carried on through several generations. Inbred sons and grandsons of the first Holstein sire used were developed as sires, and inbred daughters of these sires were used.

In the Guernsey group, the birth weight of the calves decreased as the inbreeding became more intense. A few calves were born deformed. The mature weight of the cows decreased with the inbreeding. The milk production of the inbred daughters remained about the same as that of the foundation cows. The variation between individuals, however, decreased with the continued inbreeding.

In the Holstein herd the inbreeding was not accompanied by any decline in fertility. Neither did the number of abortions nor the normality of the calves appear to be affected. The birth weight of the highly inbred calves was reduced markedly. The mortality of the inbred calves after birth was higher than in the outbred grades or registered Holsteins. The growth rate also declined with the increased intensity of inbreeding; the mature weight of the inbred cows was considerably below that of the other Holsteins reared under the same environment.

The continued inbreeding was accompanied by an increase in milk production and a decrease in the percentage of butterfat. There was, however, a marked increase in both milk and butterfat in the first generation of outbred daughters.

Waters and Lambert (1936) reported on a study, extending over a ten-year period, of the effects of inbreeding in the White Leghorn fowl. The characters receiving special attention were fertility, hatchability, viability, number of days to first egg, egg production, egg size, and body size. The degree of inbreeding for the flock as a whole was less intense than that from brother-and-sister or parent-and-offspring matings. One family, however, with the equivalent of brother-and-sister mating was maintained successfully for nine generations. The ancestry of all the birds in six families was traced to four males and seven females.

The inbreeding coefficients of the birds ranged from 41 to 82 per cent. Waters and Lambert report no general decrease in percentage of fertile eggs with the increased inbreeding. They did observe a slow but gradual decline in the average percentage hatchability of fertile eggs for all the inbreds as the inbreeding continued. The average hatchability for all inbreds, however, remained in most cases above 60 per cent. In six of the families developed there was no general decrease in hatchability.

There was a decrease in the number of days to first egg. The most highly inbred birds reached sexual maturity on an average 16 days earlier than the non-inbred foundation stock. The number of eggs laid during a given period decreased as the inbreeding increased. The 70 per cent inbred group, however, compared favorably in number of eggs laid with the non-inbred foundation stock.

Egg weight did not decline as a result of the continued inbreeding. The growth rate and adult body weight were not materially affected by the continued inbreeding.

The 80 per cent inbred group was the only group showing an increase in mortality up to 24 weeks of age. During the pullet period, however, there was a marked rise in mortality for the more intensely inbred birds with the exception of the group possessing an inbreeding coefficient of 70 per cent.

The above is one of the more encouraging reports on the experimental inbreeding of farm animals. Whereas the immediate objective of inbreeding is the improvement of genotype, the phenotype must perform sufficiently well to maintain the genotype.

The University of California has had an inbreeding project with Jersey cattle underway since 1922. The inbreeding coeffi-

cient has been brought to 0.469 (not the average). Since 1935 lethals and sub-lethals have been coming to light: imperfect epithelium, reported by Regan, Mead, and Gregory (1935); a recessive type of achondroplasia, reported by Gregory, Mead, and Regan (1942); cataract, reported by Gregory, Mead, and Regan (1943); proportionate dwarfism, reported by Mead, Gregory, and Regan (1942); flexed pasterns, reported by Mead, Gregory, and Regan (1943); and female sterility, reported by Gregory, Regan, and Mead (1946).

General Appraisal of the Above-Mentioned Experiments.

On the whole, the results of the above-mentioned experiments on farm animals may be regarded as negative. The experiment on fowl by Waters and Lambert is an exception. The results are negative at least in contrast to the results obtained on laboratory animals by King and Wright and to the practical applications made by inbreeding in modern corn production. However, this is no criticism of these earlier experiments for they have yielded extremely valuable information.

The early experiments have helped to point out the need for more rather than less inbreeding. The very fact that so many lethal and sub-lethal factors were brought to light in the California experiment with Jersey cattle shows merely what can be covered up in an outbreeding program. An objective in the constructive use of inbreeding is to uncover and eliminate the less desirable genes.

The early experiments also paved the way for improved techniques in applying inbreeding to animal improvement. It appears that the above-mentioned experiments may have yielded negative results for any or all of the following reasons:

1. Most of the early experiments were of necessity conducted on a small scale. It does not appear that an experiment of this kind is likely to be highly successful if conducted with small numbers. A small sample of foundation animals subjects the experiment to a severe handicap at the outset. If the inbreeding uncovers undesirable recessives, a small population offers little opportunity to eliminate the genes without losing the entire strain.

2. In some experiments, at least, it appears that performance was not given special consideration in the selection of breeding stock. Waters and Lambert specifically state that, in the con-

duct of their experiment, selection was most exacting for the factors affecting vigor. There is no way of knowing how the results of the other experiments would have differed if performance had been stressed, but since the inbred lines usually are lost because of poor performance in one or more respects it appears that it is sound to stress performance at the outset.

3. In most of the early experiments, attempts were made to follow definite experimental patterns such as continuous full brother \times full sister matings or half brother \times half sister matings. A fixed pattern of procedure restricts the use of superior animals to conform to the pattern. Again there is no way of knowing how much this procedure handicapped the early studies. It may have been a severe handicap. In the breeding of laboratory animals and crops the large numbers used greatly increase the likelihood of some good resulting by chance. With more restricted numbers the breeder cannot trust so much to luck; when superior breeding animals are uncovered they should be used to the maximum regardless of how they fit into the experimental pattern.

U.S.D.A. Regional Breeding Laboratories. By the early thirties sufficient information about inbreeding and its possibilities as a tool for improvement was available to enable leading administrators of research in agriculture in this country to begin planning a more concentrated attack on the problem in farm livestock. The success that had resulted from the crossing of inbred lines of corn was in a large measure responsible for the confidence of the administrators that inbreeding could and should be made to contribute to the improvement of farm animals. The result was the establishment of three Regional Breeding Laboratories, the Regional Swine Breeding Laboratory, the Western Sheep Breeding Laboratory, and the Regional Poultry Research Laboratory. The Regional Swine Breeding Laboratory was established in 1937, and the others shortly thereafter.

In 1945 national coördinated programs of breeding beef cattle and dairy cattle were initiated. The programs have much in common with those of the three regional laboratories mentioned above. Both are coördinated efforts to improve by breeding the beef cattle and dairy cattle of this nation. Both are making attempts to utilize inbreeding and intensive selection toward that end.

The objectives of the swine and sheep laboratories were to learn more about procedures in breeding for improvement. The initial work centered on inbreeding and selection with the expectation that crossing would be utilized eventually. The result desired was the development of methods that would speed livestock improvement by breeding.

An objective in the poultry laboratory was the prevention and control of avian leukosis. The attack was planned through studies of genetics, pathology, physiology, nutrition, and management. The genetic studies centered on the development of inbred lines selected for resistance to the disease.

In organizing the research program for the laboratories the weaknesses of previous research undertakings were recognized, and an attempt was made to make some corrections. The two major corrections made were that performance was emphasized in selection, and more animals were utilized. The latter was largely the reason for organizing the work on a laboratory basis, and it allowed for a broader attack.

All five of the above-mentioned programs have made notable contributions to scientific knowledge regarding inbreeding and selection. Scientific papers have been published, and definite inbred lines of livestock have been produced under the auspices of the different laboratories. More inbred lines are in the making. Some of these lines appear to be on the verge of making important economic contributions to livestock improvement in this country. The results to date indicate that livestock breeding of the future is due to change its general pattern and follow to some extent the pattern set for corn breeding. It also, however, is becoming increasingly clear that, for obvious practical reasons, the exact pattern set by corn breeders cannot be followed in all its details.

General Summary of Improvement by Inbreeding. As a whole research work indicates great possibilities for the improvement of livestock by inbreeding. Inbreeding is the quickest and most certain method of bringing out what is in a population. Inbreeding brings the recessives to light, many of which are undesirable, thus giving the breeder an opportunity to eliminate them from the population and to purify this stock for the more desirable genes.

Inbreeding also breaks up old associations of genes, especially after a wide cross, or whenever a heterozygous population is inbred. As it breaks up old gene associations it brings about new groupings, as illustrated by the usual dihybrid ratio of $AAbb \times aaBB$. This process has both desirable and undesirable results. Old associations that led to desirable gene interactions may be lost; at the same time new combinations that result in desirable gene combinations or interactions may follow.

Inbreeding is the only method known whereby purification can be carried forward. An advantage in further purification is that the crossing of more highly purified breeds or lines produces more uniform results.

The fundamentals involved in inbreeding are rather clear but much is still unknown about its applications. It is far from clear how much inbreeding is needed in livestock to obtain maximum efficiency of production in crossing. If a coefficient of inbreeding of 0.30 will do as well, or even nearly as well, in crosses as one of 0.60, there is no advantage in going to the expense and trouble of developing lines with the higher coefficients of inbreeding. It is probable, however, that the optimum coefficients of inbreeding will show considerable variation from line to line.

The optimum rate of achieving purification is not clear. The author's experience indicates strongly that lines differ in this regard. Lines developed from the crosses of other inbred lines appear to be able to absorb a faster rate of inbreeding.

Breed crosses appear to offer the greatest opportunity for the development of superior inbred lines. They offer an opportunity for inducing new gene combinations. The opportunities in this field are practically unlimited, for the genes possessed by farm animals are so numerous that it is impossible to estimate the many new combinations that may be brought about.

In corn breeding some desirable hybrids have been produced from very inferior inbreds. A parallel situation may develop in livestock, but there are several reasons why it is more difficult for a livestock program to succeed with poorly performing inbred lines. Livestock are not nearly so prolific as corn. One kernel of corn can produce a plant with an ear of corn that has 1,000 or more kernels. Poultry are the most prolific farm animals but they are far less prolific than corn. This factor alone prohibits the use of animals markedly inferior in any of the factors of

performance. Furthermore the cost of maintaining the inbred lines would be prohibitive as a practical procedure.

It is generally assumed, with considerable supporting evidence, that superior traits tend to arise from dominant genes. It would therefore appear that by the development of superior inbred lines more desirable genes would be made pure and retained than by the selection of inferior lines. Thus when the superior lines are crossed more desirable genes should be put in the cross.

A limiting factor to the above reasoning is that gene interaction may make some genes that are undesirable by themselves valuable when in association with other genes. Nevertheless, the limited crossing studies in livestock to date indicate that the superior inbred lines and superior individuals on the average produce the best crossbreds. Studies of corn by Hayes and Johnson (1939) and Johnson and Hayes (1940) support the above generalization.

Inbreeding automatically reduces the vigor of the stock so bred: it is hybrid vigor in reverse. The constructive breeder then tends to offset this general effect of inbreeding by rigorous selection for improved performance. If the selection is successful the breeder will hold the performance in balance. It is possible that some highly inbred lines will be developed that greatly exceed good outbred stock in performance. However, this is not likely to occur without considerable effort. The success of the selection is dependent upon accumulating enough additional additive gene effects to offset the loss caused by a decrease both in dominance and gene interaction. It appears that inbreeding to the lower levels (F_x 's of about 25 to 35 per cent) can be attained without any noticeable loss of vigor; in fact some may be gained. A major result of this stage of inbreeding when complemented with stringent selection is likely to be a reduction in the size of the various allelomorphic series and the elimination of many of the less desirable genes. On the other hand, the degree of homozygosity attained may be less than theoretically indicated.

The final measure of the value of an inbreeding program or of inbred lines is what purpose has been or can be served. Present-day thought is that the final measure of an inbred line's usefulness is what it will do in crosses with other inbred lines or outbred stock. This is only a partial answer, for it is also dependent on the cost of maintaining the inbred line. Inbred lines

that are overly costly to maintain are not likely to be economically sound for crossing even though they cross well. On the other hand, some of these same inferior inbred lines may possess genes that will be valuable for the improvement of other inbred lines. In still other instances, some inbreeding may prove very valuable merely as a means of reducing the size of the allelomorphous series and ridding the stock of the many less desirable genes. Final appraisals of inbreeding cannot be assessed by the same scale of values; each inbred line should be appraised by the question, "Did the program accomplish, in part at least, what it was planned to do?"

Crossbreeding

Crossbreeding is the opposite of inbreeding; it promotes the pairing of unlike genes by the mating of animals that belong to different families, breeds, or species. The crossing of animals that belong to different families within a breed is often spoken of as outcrossing. Actually the difference between the crossing of families or breeds and the crossing of breeds and species is merely one of degree on a sliding scale. In this respect it is comparable to the difference between inbreeding and linebreeding.

Inbreeding and crossbreeding are part of the same phenomenon. The results of both are explained by Mendel's laws and the interpretation of hybrid vigor.

Objects of Crossbreeding. Crossbreeding is the third tool the animal breeder has with which to work toward genetic improvement. The other two are selection and inbreeding. Genetic improvement can come only through the sorting out of the genes which produce the most desirable results and by bringing together the gene combinations that yield the most desirable effects.

The history of animal breeding and more recently the constructive work of the plant breeders have demonstrated that crossbreeding is a tool to be used for genetic improvement. In general animal breeders have been reluctant to recognize the possibilities in crossbreeding. This situation, however, has been changing since about 1935.

The chief reason for crossbreeding is to bring about an increase in vigor. Vigor is used in this connection to cover almost everything that pertains to desirability. The main items are rate of gain, economy of gain, fertility, and general strength. It has also been rather generally assumed that these desirable traits are stimulated largely by dominant genes. The reasons for this belief are that the characters possessed by wild-type animals

are largely dominant and that the explanation of hybrid vigor rests on dominance.

Nevertheless, some care must be exercised in making the above generalization lest we take too much for granted. The animal traits most useful to man may not be compatible with the traits that are most desirable to the animal under natural conditions. A high degree of fertility is very desirable in the domestic animal. Under natural conditions 10 pigs in a litter and twin lambs may be liabilities. The race that produces a more limited number of young, but young that are stronger at birth, may be better suited to survive. Heavy milk flow is an advantage when the female is well cared for, but under natural conditions it may lead to damaged udders and the production of contaminated milk. A rapid rate of growth is desirable in the production of market animals, but in the wild it may be a handicap. The fast-growing animal requires a larger daily intake of food than the slow-growing animal. Under natural conditions an abundance of food may often be lacking, and the animal with the inherent capacity for rapid growth is handicapped more than the one with less capacity for growth. The same general principle applies to adult size.

An illustration of this point is to be found in the development of the Piney Woods pig. These are pigs running loose in the woods and swamps of many parts of the southern part of this country. Presumably they are descendants of the early pigs brought over by Spanish and French settlers. No doubt from time to time their gene complex has been disturbed by the addition of genes introduced by pigs that escaped or were turned loose from the adjacent farms. The latter are usually descendants of the more popular American breeds of swine. Nevertheless, as the result of natural selection, many of the Piney Woods pigs reach an adult size of a little over, or even less, than 100 pounds (Fig. 68). Not only the size but also the proportionate body parts are in marked contrast to that of a modern pig (Fig. 69). From the farmer's standpoint, the Piney Woods pig would not be classified as especially desirable or vigorous. Yet under natural conditions where he must look after himself he possesses a type that apparently is closely associated with vigor for that special environment.

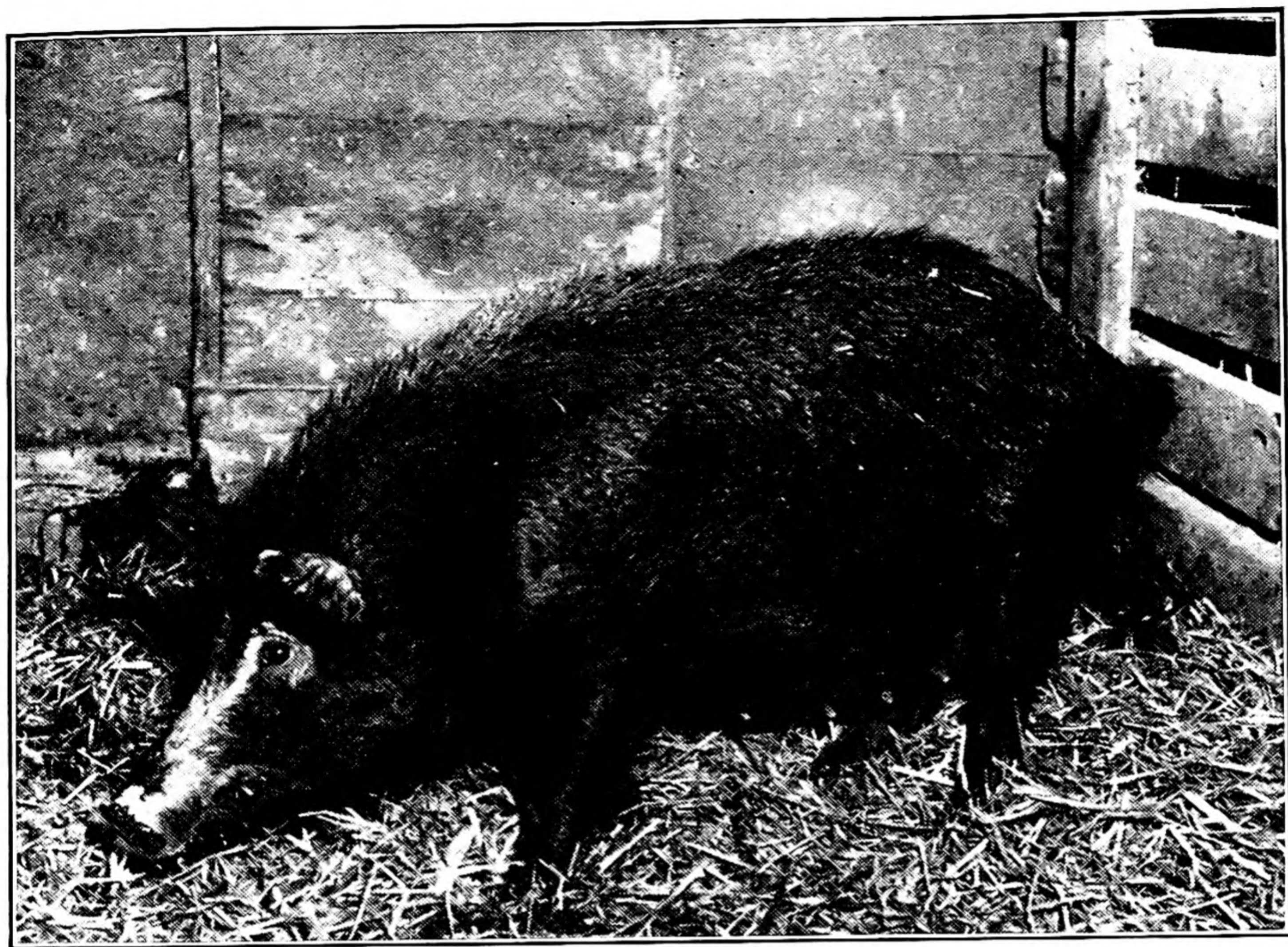


FIG. 68. A Piney Woods pig—a type well adapted to a very special environment.

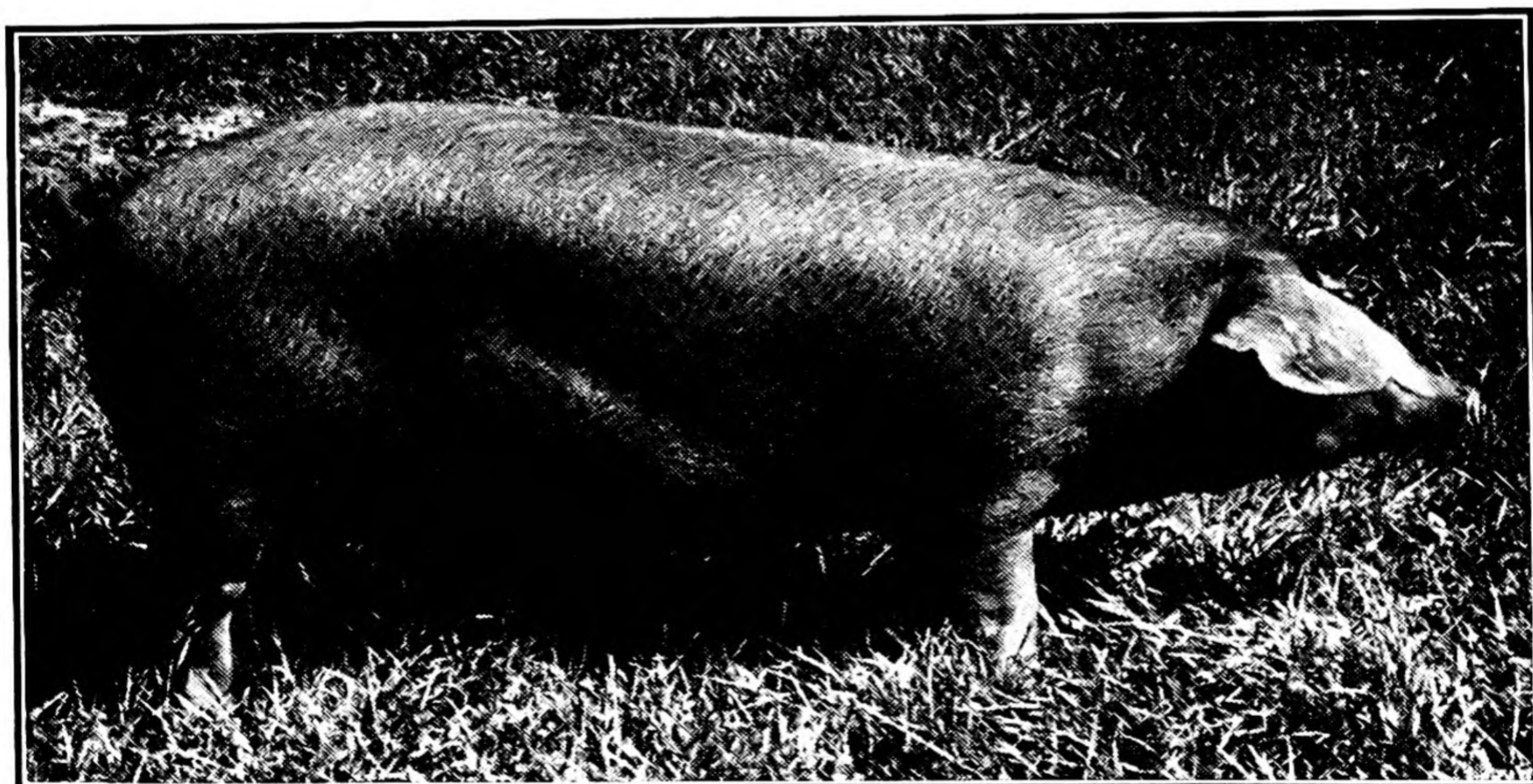


FIG. 69. A modern-type pig, Minnesota No. 1, developed for a special purpose and environment. Contrast with Fig. 68.

The chief reason for including the above at this point is to point out that vigor may mean different things under different conditions and that it is well to exercise some care in the generalizations drawn from wild types. The fact remains that crossbreeding generally results in an increase in all the elements of vigor, as measured under domestic conditions. A large portion of this increase is due to bringing more dominant genes into play.

It has frequently been stated that inbreeding produces uniformity and crossbreeding produces variability. A statement of this type causes confusion unless it is well qualified. As a rule first and second crosses yield very uniform populations. Inbreeding if continued leads to the development of families and subfamilies the members of which are remarkably uniform, but the immediate results of inbreeding a heterozygous population is the segregation of both phenotypes and genotypes.

Crossbreeding promotes the pairing of unlike genes, and it is used for the following reasons:

1. A single cross is used to introduce new genes in a closed population. The closed population may be a closebred family or a breed. Crossbreeding is a logical procedure in constructive animal breeding. Unfortunately, however, this method of constructive breeding can be used in breed improvement only by clandestine methods; and it has been used rather frequently. It would, however, be much better if the method could be used openly and yet with sufficient restrictions to keep the procedure within control.

If a certain breed, or family within a breed, is deficient in a certain trait, the quickest and most certain method of improving that trait is to introduce genes through crossbreeding to some stock known to be superior in the trait. The counterargument often advanced is that every breed has all the genes necessary to make, within reason, whatever is desired from the breed. Even if this statement is correct, which has never been proved, it is absurd to take many years to do a job that can be done in less time by an improved technic.

The above-mentioned type of crossing is often spoken of as outcrossing, and it is not foreign to livestock breeders; Lovejoy, the Colling brothers and Bakewell, among others, used it freely. It is a method that is used regularly by many of the best breeders of Hill sheep in Scotland (page 383). Most animal breeders,

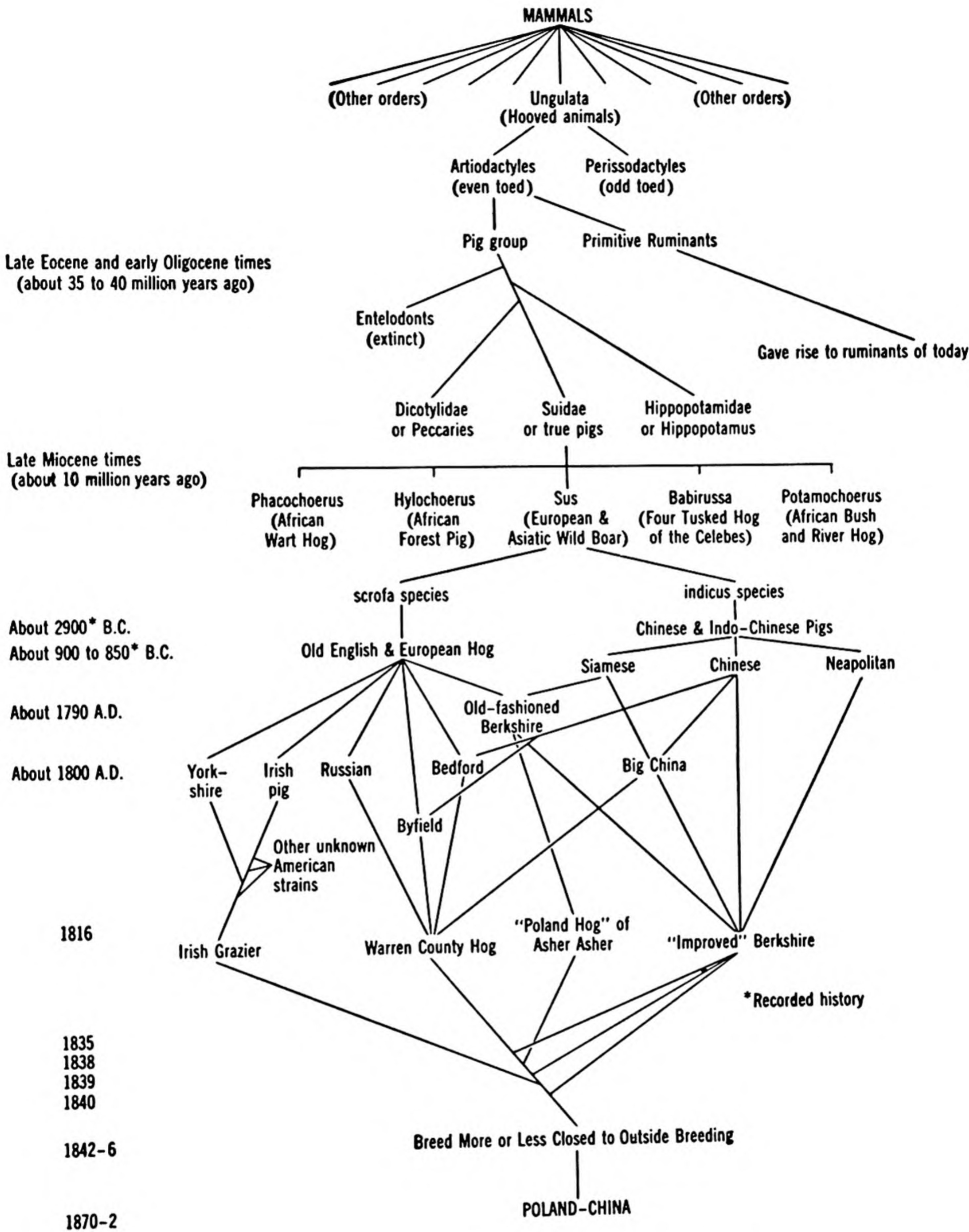
however, use it in a limited way only, at least when they use it legally, that is, by staying within their own breed. This does not give the breeder the full latitude that can be provided by selecting genes wherever useful genes may be found. Plant breeders have made deliberate and more frequent use of this method than animal breeders in recent years. Gametic selection as proposed by Stadler (1944 and 1948) is but a slight modification of this method. It appears almost certain that animal breeders in the future will be using this technic much more in an attempt to improve the present inbred lines that have been and are being developed.

2. A second reason for crossbreeding is to make the crossbreds the basis of a new breed. The majority of our present improved breeds originated from crossbred foundations (Fig. 70). For about 50 years crossing for this reason has been generally frowned upon in livestock circles, and breed promoters have attempted to present evidence that their breed has been pure from time immemorial. Usually this attitude is the result of presenting only a part of the evidence available regarding both breed history and the history of the human race. It is also the result of a failure to recognize the biological laws of inheritance.

Ultimately it makes no difference how long a breed or strain has been bred from within, for the value of the breed or strain depends on what can be done with it. Obviously the genes are put in a more heterozygous condition by crossing. Subsequent inbreeding from such a population offers opportunity for segregation. New gene groupings are thereby created, and an opportunity is offered for more desirable gene groupings than existed formerly. Not all new gene groupings will be more desirable. There is no reason why they should be, but by creating new gene combinations the constructive breeder has the opportunity of selecting improved types.

3. The major reason for crossbreeding is to produce market animals.

Hybrid Vigor. Both practical and experimental breeders of plants and animals have long recognized heterosis or hybrid vigor. Whaley (1944) states that hybrid vigor has been recognized for at least two and a half centuries. Only during the past three decades, however, has our understanding of the cause of hybrid vigor been clearing.



ANCESTRY OF THE POLAND CHINA BREED OF SWINE

FIG. 70. Ancestry of the Poland China breed of swine. (Courtesy Dr. Elwood Stringam.)

Jones (1917 and 1918) advanced the theory that has become known as the dominance of linked factors hypothesis. Whaley (1944) stated, "Jones made what still stands as the most thorough study of the genetic aspects of the heterosis problem." This theory rests on the assumption that vigor is dominant to lack of vigor and that the individuals crossed differ in certain

P_1

X									
I		I		II		II		III	
A	1	A	G	1	G	M	1	M	
b	$\frac{1}{2}$	b	h	$\frac{1}{2}$	h	n	$\frac{1}{2}$	n	
C	1	C	I	1	I	O	1	O	
d	$\frac{1}{2}$	d	j	$\frac{1}{2}$	j	p	$\frac{1}{2}$	p	
E	1	E	K	1	K	Q	1	Q	
f	$\frac{1}{2}$	f	l	$\frac{1}{2}$	l	r	$\frac{1}{2}$	r	

$4\frac{1}{2}$
+
 $4\frac{1}{2}$
+
 $4\frac{1}{2} = 13\frac{1}{2}$

Y

I'		I'		II'		II'		III'		III'	
a	$\frac{1}{2}$	a	g	$\frac{1}{2}$	g	m	$\frac{1}{2}$	m			
B	1	B	H	1	H	N	1	N			
c	$\frac{1}{2}$	c	i	$\frac{1}{2}$	i	o	$\frac{1}{2}$	o			
D	1	D	J	1	J	P	1	P			
e	$\frac{1}{2}$	e	k	$\frac{1}{2}$	k	q	$\frac{1}{2}$	q			
F	1	F	L	1	L	R	1	R			

$4\frac{1}{2}$
+
 $4\frac{1}{2}$
+
 $4\frac{1}{2} = 13\frac{1}{2}$

F_1

I		I'		II		II'		III		III'	
A	1	a	G	1	g	M	1	m			
b	1	B	h	1	H	n	1	N			
C	1	c	I	1	i	O	1	o			
d	1	D	j	1	J	p	1	P			
E	1	e	K	1	k	Q	1	q			
f	1	F	l	1	L	r	1	R			

6
+
6
+
6 = 18

FIG. 71. Illustrating how dominant factors contributed by each parent may enable the crossbred to attain a greater development than either parent. (Modified from Jones in *Genetics in Plant and Animal Improvement*, John Wiley & Sons.)

factors which contribute to vigor. It is also assumed that factors for vigor are linked with factors for lack of vigor or less vigor. In the theoretical illustration (Fig. 71) it is assumed that the individuals X and Y are each homozygous and that three pairs of chromosomes carry factors for vigor which are equal but different and occupy different loci. The factors for vigor in X are labeled A , C , E , G , I , K , M , O , and Q ; and those for vigor in Y are labeled B , D , F , H , J , L , N , P , and R . It is assumed that the genes A , B , C , and so on, are dominant to their alleles a , b , c , and so on. In the illustration the complete dominance of vigor is assumed, but if vigor is only partially dominant to lack of vigor the same effect, heterosis, is produced. That vigor is dominant or partially dominant to lack of vigor is today

more than an assumption, for from inbreeding experiments it is clear that undesirable factors are much more frequently recessive than dominant.

In order to simplify the above illustration the number of genes and chromosomes was kept low. Actually Jones's original assumption was that many genes were involved and that they were widely distributed among the total chromosome number. It is now well known that many genes are involved in the expression of such characters as size, rate of growth, and fertility.

Powers (1944) advanced what he proposed to call an expansion of Jones's theory of heterosis. Powers reported that crosses in tomatoes are influenced by size and number of fruit. In a cross of two inbred lines, 4102 and 4110, the F_1 were not only below the better parents in each respect but in both respects they were below the means of the two parents, yet in yield the hybrid exceeded the high parent by a substantial margin.

TABLE XXV. NUMBER OF RIPE FRUIT, SIZE OF FRUIT, AND YIELD OF RIPE FRUIT OF A TOMATO HYBRID AND ITS PARENTAL LINES

(From Powers, *American Naturalist*)

Hybrid or Inbred Line	Ripe Fruit, Number	Size, Grams	Yield
4102	4.4 \pm 0.69	138 \pm 12.81	607 \pm 86
4110	109.1 \pm 11.34	17 \pm 0.58	1,868 \pm 149
F_1	44.5 \pm 2.52	55 \pm 2.93	2,428 \pm 150

Richey (1942) had previously made a comparable report on height of plants. Two plant varieties will be of equal height if one has twice as many internodes of half the length of the other. A cross of the two will produce a hybrid which will exceed their height by 12.5 per cent if internode number and length are exactly intermediate in inheritance. Richey points out that the same principle applies to other characters such as yields of grain, leaf area, and growth rate.

The condition of heterozygosity itself has always presented an especial appeal as an explanation for heterosis. Stubbe and Pirschle (1940) cite evidence to support that view. They worked with a race of *Antirrhinum majus* that exhibited a chlorophyll deficiency. The race possessed a tendency to mutate back to normal. By selfing individuals were produced which were heter-

ozygous with respect to the mutant gene and exhibited some hybrid vigor. This they give as evidence that heterosis is due to heterozygosity itself.

Singleton (1943) reports an instance of heterosis due to a single factor difference. An inbred strain of sweet corn *P39* mutated to a dwarf form *C30*. Crosses between *P39* and *C30* indicated that a single recessive mutation was involved. Crosses of the mutated form *C30* with other inbreds, *C13* and *C15*, gave higher yields than crosses of the normal form *P39* with *C13* and *C15*.

Jones (1945) reports on instances of heterosis resulting from degenerative changes. Six recessive mutations appeared spontaneously in five inbred lines of maize. All of the six reduced the amount and rate of growth in some respect and were classed as degenerative changes. The evidence indicates that each one differs from the normal homozygous line from which it originated by a single allele. When the reduced mutant lines were crossed with the parental normal line from which they arose heterosis resulted. Jones states: "Heterosis is interpreted as an accumulative effect of favorable heredity from both parents. This results even when only single allelic differences are involved provided genes have multiple effects."

Oliver and Green (1944) found heterosis in what they call compounds of lozenge alleles in *Drosophila melanogaster*. Their

TABLE XXVI. VIABILITY, FERTILITY, AND FECUNDITY OF LOZENGE ALLELES

(From Oliver and Green, *Genetics*)

Type	Number Mated	Viability			Fertility			Fecundity			
		No.	%	S.E.	No.	%	S.E.	No. F_1	%	S.E.M.	S.D.
lz^a	899	747	83.1	1.25	173	23.2	1.54	1,616	9.3	0.79	10.4
lz^s	496	142	28.6	2.03	50	35.2	4.01	755	15.1	1.77	12.5
lz	523	211	40.3	2.14	61	28.9	3.12	482	7.9	1.21	9.5
lz^g/lz^a	468	430	91.9	1.26	209	48.6	2.41	5,503	26.3	1.34	19.4
lz^g/lz	455	371	81.5	1.82	131	35.3	2.48	2,775	21.2	1.58	18.1
lz^s/lz	196	165	84.2	2.61	79	47.9	3.89	1,966	24.9	2.28	20.4

results, presented in Table XXVI, show clearly that viability, fertility, and fecundity were greatest in the compounds.

Oliver and Green are of the opinion that modifying genes affected the factors concerned. This is another way of stating belief in heterosis as the result of the interaction of genes other than alleles. They contend also that the data indicate that heterosis is the result of the interaction of the recessive lozenge alleles when put in a compound.

Hull (1945) has introduced the term “overdominance” (see page 121) to describe that condition wherein the heterozygote exhibits a greater amount of the character in question than the individual that is homozygous for the dominant gene. A simple illustration of the interrelationship of overdominance, dominance, partial dominance, and lack of dominance is given below with the assumed numerical values for the different genetic states:

<i>AA</i>	<i>aa</i>	<i>Aa</i>	
10	4	12	Overdominance
10	4	10	Dominance
10	4	8	Partial dominance
10	4	7	Lack of dominance

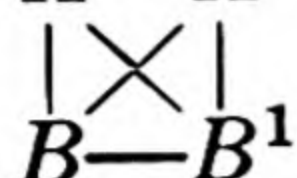
The discovery that overdominance does occur has resulted in a great deal of speculation in regard to means whereby it may be used to bring about more hybrid vigor than has been general up to this time. Overdominance apparently is the result of both the interaction of allelic genes and increased non-allelic action, for the *AaBB* state offers opportunity for both *A* and *a* to interact with *B*. Most likely, groups of genes usually allow for the interaction between both alleles and non-alleles. Genetic interaction between alleles and non-alleles is today, then, a well-established fact. However, the mechanism that makes genic interaction possible is not clear. It is not clear whether, in the above illustration, *A* provides one sort of stimulant and *a* a different stimulant, with the result that the two when combined provide a greater stimulation than two doses of either one alone or whether *Aa* enters into some sort of chemical reaction which thereby results in a greater boost than a double dose of either *A* or *a*.

The heterozygous state certainly offers much greater opportunity for the interaction of genes than the homozygous state.

Let it be assumed that we are dealing with a case of gene interaction; the individual that is $A A$ has the opportunity only for



an interaction between A and B . On the other hand, the individual that is $A-A^1$ has opportunity for six different interactions.



If, however, we fully accept belief in the manifold effects of the gene and genic interaction and believe that the genes achieve their results by a series of chemical reactions, the number of possible genic interactions is greatly increased in moving from the genotype $AABB$ to AA^1BB^1 . In the latter genotype the following genic interactions are possibilities:

$A-A^1$	A^1-B	$B-B^1$	B^1-AA^1
$A-B$	A^1-B^1	$B-AA^1$	B^1-AB
$A-B^1$	A^1-AB	$B-AB^1$	B^1-A^1B
$A-A^1B$	A^1-AB^1	$B-A^1B^1$	B^1-AA^1B
$A-A^1B^1$	A^1-BB^1	$B-AA^1B^1$	
$A-BB^1$	A^1-ABB^1		
$A-A^1BB^1$			

Objection can be raised to the above on the basis that it includes repetitions, for example, $A-A^1B$, A^1-AB , and $B-AA^1$. However, there is the possibility that A^1B may first enter into a reaction and later react with A . In like manner there is the possibility that AB may enter into a reaction that later reacts with A . The idea of chain reactions receives support from the fact that the individual is affected throughout life by its genetic state, yet its genetic state remains constant.

It is well recognized that the individual is the result of genic interaction with environment. If this is added to the above, the possibilities become enlarged still more.

Crossing Breeds. The systematic crossing of breeds has long been practiced in Europe. In the British Isles blue-gray cattle, Aberdeen-Angus-Shorthorn or Galloway-Shorthorn, have long enjoyed an enviable reputation both in the show ring and on the markets. Many of the breeds of sheep are also crossed for the production of market lambs. One of the most prominent of these is the Border Leicester-Cheviot. The halfbred ewes, as they are known, are about the most popular ewes in the British Isles for commercial production. The ewes are usually bred to a

ram of a third breed. Suffolk and Oxford Down rams are popular choices.

In the United States many corn belt farmers have for years practiced the crossbreeding of hogs. In the third edition of this book (1939) this statement was made: “. . . in many cases mixing the breeds might better describe the method, for systematic crossing has not been the rule, but this is changing.” The situation has changed markedly since 1939; many hog raisers are now quite systematic in their crossbreeding. Estimates indicate that more than 80 per cent of the hogs reaching our central markets are crossbreds.

Many range sheep producers have long been systematic in crossing the breeds. In many instances longwool rams are crossed to grade finewool ewes; the crossbred ewes are maintained and bred to Down rams for the production of market lambs. Range men who follow this practice contend that a crossbred flock is a more profitable one than a finewool, because the ewes are larger and stronger, raise a larger lamb crop, and produce a fleece which is high in quality and quantity. The Down ram gives to the lambs a blockiness of type, which is so prized on the markets.

In general, it may be said, popular opinion is that the crossbred matures earlier, requires less feed, is more vigorous, and is in general superior to either parental type.

Experimental Crossbreeding. Through the years many reports have shown an advantage in favor of crossbreds. For the most part the early individual experiments were limited in scope and attracted little attention. Nevertheless these early experiments almost without exception showed an advantage in favor of the crossbreds. Many commercial livestock producers continued to crossbreed even though they were usually advised that crossbreeding was a poor practice.

The Minnesota Experiment with Swine. In order to obtain definite information regarding the merits of crossbreeding, in the fall of 1928 the Minnesota Experiment Station began a study of crossbreeding (Winters *et al.*, 1935). The experiment was conducted on a large scale and in a very exacting manner. The purpose was to answer the following questions:

1. How much added vigor may a farmer expect as the result of crossing two or more breeds of swine?

2. Should the crossbred gilts all be marketed, or can they be used to advantage for further breeding?

3. If the crossbred sows are better mothers, how can they best be used for further breeding?

The experiment was conducted independently at two separate points, but the work at the two locations was coordinated and the study covered a six-year period.

Spring-farrowed boars and gilts were used exclusively as breeding stock throughout the experiment. The plan of matings was so organized that similar genetic material was used in the purebreds and in the crossbreds. The comparison therefore was designed to determine if it made any difference whether the same genetic material was used to produce purebreds or crossbreds. The phrase, the same genetic material, needs to be interpreted in a broad way because it is well recognized that purebreds are not pure genetically. However, if enough matings are made, the average of the genetic material put in the crossbreds will be about the same as that put in the purebreds. If the average is not the same, the purebreds are so variable genetically that there would appear to be no value in going to the trouble and expense of maintaining the purebreds as such.

The following types of matings were made in the Minnesota experiment:

West Central Experiment Station

Poland China boar \times Poland China gilts

Duroc boar \times Poland China gilts

Poland China boar \times Duroc gilts

Duroc boar \times Duroc gilts

Northwest Experiment Station

Chester White boar \times Chester White gilts

Duroc boar \times Chester White gilts

Chester White boar \times Duroc gilts

Duroc boar \times Duroc gilts

The same boars sired both the crossbreds and the purebreds. The gilts of each breed group for each station were purchased from the same herd and averaged about three-fourths sisters in relationship.

The above matings were repeated in the second and third years, and the following matings were made in addition:

West Central Experiment Station
Chester White boar × Poland China-Duroc gilts

Northwest Experiment Station
Poland China boar × Chester White-Duroc gilts

The boars used in the above three-breed cross were in each case from the purebred herd of the other station. This was done to keep the breeding as nearly comparable as possible.

In the fourth year of the experiment and for the last three years, the Yorkshire breed was substituted for the Chester White and the Poland China for the Duroc at the Northwest Experiment Station. An additional cross was made at each station by mating the crossbred gilts back to one of the parental breeds. The resulting individuals were designated as back-cross pigs.

The above types of matings gave pigs of four types of breeding:

- Purebreds—four breeds
- First cross
- Back cross
- Three-breed cross

Farrowing results are presented in Table XXVII.

TABLE XXVII. FARROWING RECORD, CROSSBRED AND PUREBRED
(From Winters, Kiser, Jordan, and Peters, *Minn. Bul.* 320)

Breeding	No. of Sows	No. of Individuals	Birth Weight per Live Pig, Pounds	Total Litter Weight of Live Pigs, Pounds	No. of Live Pigs	No. of Dead Pigs	Total Litter Size
Average of purebreds	76	715	2.45	20.98	8.26	1.15	9.41
Purebreds proportioned by breeds to the breeds entering in first cross	76	715	2.55	21.14	8.29	1.11	9.40
First cross	45	440	2.60	23.97	9.22	0.56	9.78
Purebreds proportioned by breeds to the breeds entering in the three-breed cross	76	715	2.58	21.21	8.22	1.18	9.40
Three-breed cross	24	245	2.59	25.59	9.88	0.33	10.21
Purebreds proportioned by breeds to the breeds entering in the back cross	76	715	2.54	21.13	8.32	1.12	9.44
Back cross	16	135	2.91	23.66	8.13	0.31	8.44

The results of the nursing period are given in Table XXVIII.

TABLE XXVIII. NURSING PERIOD, CROSSBRED AND PUREBRED

(From Winters, Kiser, Jordan, and Peters, *Minn. Bul.* 320)

Breeding	No. of Pigs Weaned	No. Lost per Litter	Litter Size at Weaning	Weight per Pig, Pounds	Total Litter Weight, Pounds
Average, all purebreds	531	2.72	5.54	28	155
Purebreds, proportioned by breeds to breeds in first cross	531	2.67	5.62	28	157
First cross	317	3.27	5.95	33	196
Purebreds, proportioned by breeds to breeds in three-breed cross	531	2.56	5.66	28	158
Three-breed cross	186	2.17	7.71	33	254
Purebreds, proportioned by breeds to breeds in back cross	531	2.75	5.57	29	162
Back cross	100	1.88	6.25	36	225

The advantages in rate and economy of gains of the crossbreds over the purebreds are given in Table XXIX, and an over-all summary of the crossbreds' advantages are given in Table XXX.

Five major factors affect productivity in swine: (1) number born alive, (2) survival, (3) rate of gain, (4) economy of gain, and (5) merit of the finished product. In the above experiment the hogs were not scored on conformation at the completion of the trial. If the other four factors affecting productivity are pooled at equal value and the figures are taken from Table XXX, the average advantages of the crossbreds over the purebreds are first cross 7 per cent, back cross 6 per cent, and three-breed cross 17 per cent. By a different method of handling the same data, in the author's opinion a more satisfactory method, the advantages over purebreds are first cross 6.3 per cent, back cross 7.5 per cent, and three-breed cross 11.7 per cent.

TABLE XXIX. ADVANTAGES, RATE, AND ECONOMY OF GAINS OF CROSSBREDS OVER PUREBREDS

(From Winters, Kiser, Jordan, and Peters, *Minn. Bul. 320*)

Breeding	No. of Lots	No. of Individuals	Feedlot Period		Birth to 220-Pound Weight	
			Pounds Daily Gain	Less Feed per 100 Pounds Gain	Fewer Days to Reach 220 Pounds	Fewer Pounds Feed per 220-Pound Pig
Purebred	21	353				
First cross	15	229	0.12	12.68	17	27.90
Three-breed cross	8	173	0.11	16.21	17	35.66
Back cross	5	93	0.14	12.15	22	26.73

TABLE XXX. SUMMARY OF ADVANTAGES OF CROSSBREDS OVER PUREBREDS IN PERCENTAGE

(From Winters, Kiser, Jordan, and Peters, *Minn. Bul. 320*)

	First Cross	Three-Breed Cross	Back Cross
Birth weight per live pig	1.96	0.39	14.57
Birth weight per litter of live pigs	13.39	20.65	11.97
Number of live pigs per litter	11.22	20.19	-2.34
Total number of pigs per litter	4.04	8.62	-11.85
Number of pigs weaned per litter	5.87	36.22	12.21
Litter weight at weaning	24.84	60.76	38.89
Saving in feed	2.99	3.85	2.91
Saving in time to reach 220 pounds	8.67	8.63	11.28

No one has yet developed an entirely satisfactory method of appraising the over-all comparative merit of swine by which two groups can be compared, as hybrid and open-pollinated corn are compared on yield. An important point, however, derived from the above-mentioned experiment is that the crossing of American

breeds of swine did yield hybrid vigor very consistently. A second point was that the crossbred females were valuable as breeders; therefore, if full advantage is to be made of hybrid vigor in livestock production, crossbred females need to be utilized as breeders.

The above conclusions are in perfect accord with modern genetic information, for on the average the hybrid may be expected to be more vigorous than the non-hybrid and, since the young animal is dependent on its mother for considerable time before and after birth, it is logical that the crossbred mother will possess added vigor for this work.

The applications of genetics to livestock breeding differ in many respects from its applications to plant breeding. In the production of hybrid corn, it has become rather standard practice to use four inbred strains which are first combined in two single crosses ($A \times B$ and $C \times D$); the two single crosses are then combined in a double cross ($AB \times CD$) which yields the seed that produces the hybrid corn. In some instances an inbred male parent is used in place of the crossed lines for the second cross. In either case it is standard practice to go no further with this stock for crop production. Similar procedure is not applicable to livestock production, at least under prevailing cultural methods. Corn is much more prolific than livestock. One kernel of corn will produce an ear with about 1,100 kernels, each of which may produce a plant that is bisexual. In contrast one sow, under favorable conditions, may raise 10 pigs, of which half are gilts, but, under average conditions, the sow will raise 3 or 4 gilts per farrowing. In cattle and horses each female will average less than 1 female every two years, and in sheep the average will be one-half to three-fourths of a female offspring per breeding female per year.

The above differences in fertility alone are sufficient to make impracticable the direct transfer of the methods used in producing hybrid corn to livestock breeding, with the possible exception of poultry. The fundamentals, however, remain the same. Because of the above-mentioned difference between corn and swine and because of the definite hybrid vigor exhibited in the above experiment Winters *et al.* (1935 and 1936) recommended two methods by which the farmer may carry on a continuous

program of crossing. The two methods were called crisscrossing and rotation crossing.

Crisscrossing calls for the alternate use of boars belonging to two breeds. The pedigree of a pig bred by five generations of crisscrossing is presented in Fig. 72.

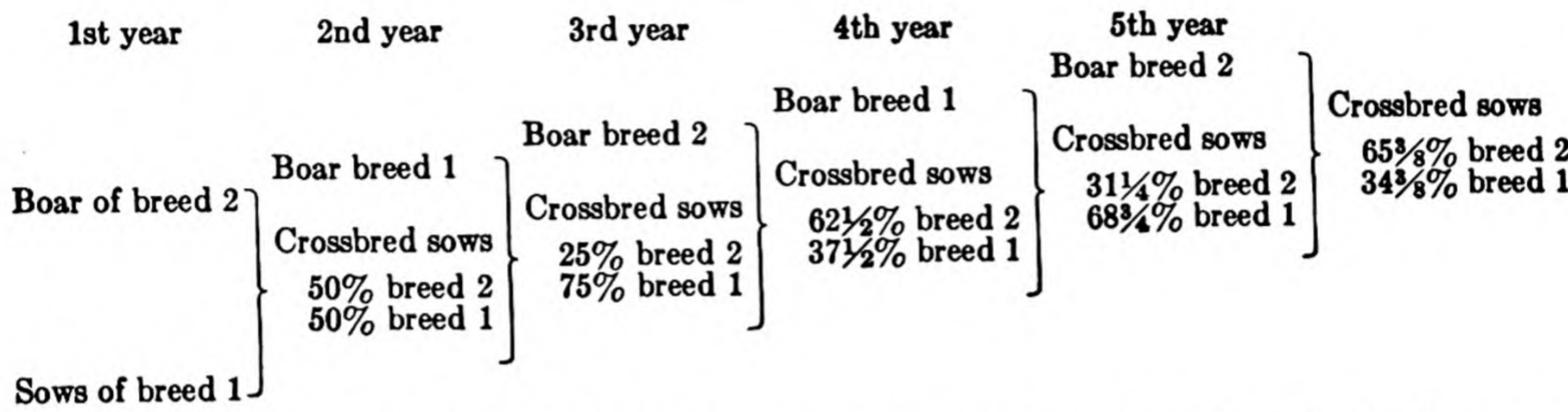


FIG. 72. The method of procedure in crossing with two breeds (crisscrossing). The approximate percentage of each breed represented in the respective generations of crossbreds is indicated.

Three or four breeds are involved in rotation crossing. The pedigree of a pig bred by five generations of rotation breeding with three breeds involved is presented in Fig. 73.

Objection to the practicability of both of the above plans has been raised (Rice, 1942) on the grounds that it necessitates breeding almost exclusively from gilts. Since most market hogs

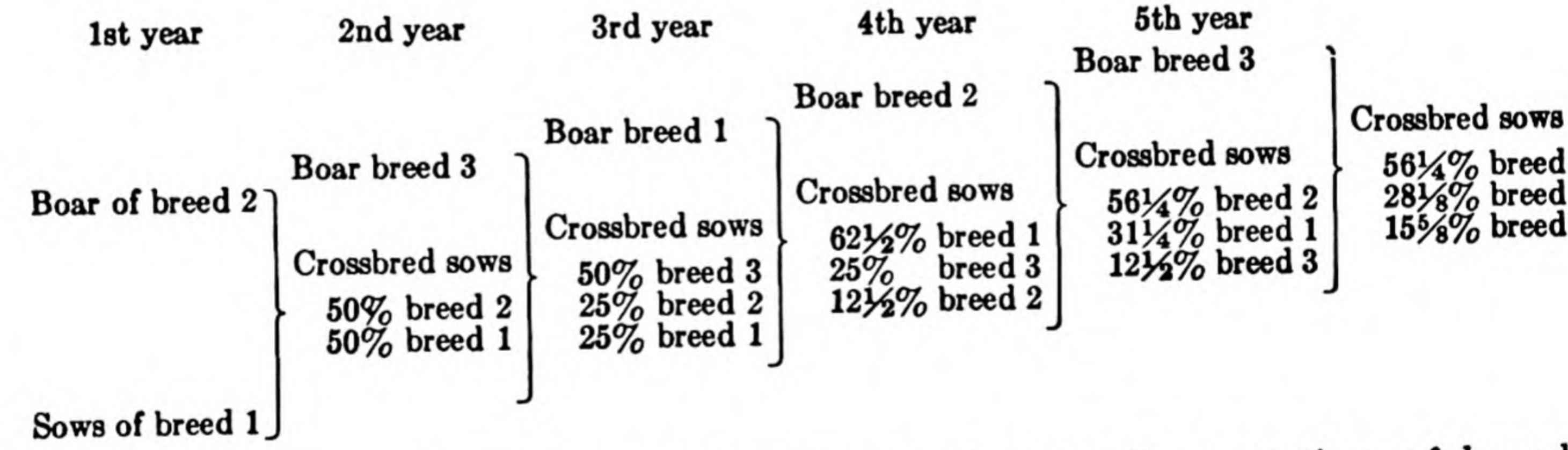


FIG. 73. The method of procedure in crossing by the rotation of breeds. The approximate percentage of each breed represented in the respective generations of crossbreds is indicated.

are produced by gilts that objection is not a serious one. Rice also states, “. . . it seems questionable whether the generally less than 10 per cent advantage in rate and efficiency of growth in the crossbreds due to heterosis is great enough to warrant its wide adoption.” Perhaps the best answer to this objection is that since first recommended (1935) it has been generally ac-

cepted by swine producers and is widely used in the swine-producing area of this country. Quaife (1946) reported the records made by the 100 master swine producers of Iowa for 1945. He stated, "Crossbreeding was practiced by 90 out of the 100 master swine producers, there being but 10 who raised straight breeds. In most cases cross-bred sows of mixed breeding were used."

Any method whereby an increased production of 10 or 12 per cent can be gained by so simple a procedure as using a male of a different breed is well worth while in any industry. It is the author's opinion that not only in animal breeding but also in our entire program of improved agriculture, we shall need to take advantage of methods that yield only 5 per cent improvement or less.

The Iowa Experiment with Swine. Lush, Shearer, and Culbertson (1939) reported on a crossbreeding trial that in many respects paralleled the Minnesota trial. Some of the data were gathered on litters from sows that were double mated, mated to a boar of her own breed and to a boar of another breed; a litter thus produced therefore contains both purebred and crossbred pigs. This procedure for studying crossbreeding has some advantages and some distinct disadvantages in execution. It is practically impossible to carry out double matings in testing crisscross or rotation breeding. The unevenness of distribution of crossbred and purebred pigs within first-cross litters leads to difficulties of execution.

A summary of the results obtained in the Iowa experiment follows:

1. The percentage of stillborn pigs was less among the crossbreds than among the purebreds.

2. The crossbred pigs exhibited more vigor at birth than the purebreds as shown by their ability to survive to weaning age.

3. The crossbred pigs averaged about 3 to 4 pounds heavier at weaning than the purebreds. The crossbred litters averaged heavier than the purebreds because the individual pigs averaged heavier and because they averaged more pigs per litter.

4. The crossbred pigs made more rapid gains in the feed lot than the purebreds. The crossbreds gained about 0.09 to 0.12 pound more per day. This is slightly less than the advantage obtained in the Minnesota experiment.

5. The crossbreds reached a market weight of 225 pounds on 25 to 30 pounds less of feed.

6. The crossbred sows were efficient pig producers.

The U.S.D.A. Experiment. Hutton and Russell (1939) conducted a crossbreeding trial which extended from 1927 to 1932. A summary of data on the production of weaned pigs is presented in Table XXXI.

TABLE XXXI. A SUMMARY OF PRODUCTION DATA ON WEANING OF PUREBRED AND CROSSBRED PIGS

(From Hutton and Russell, *U.S.D.A. Cir. 532*)

Breed	Sows Bred, No.	Litter Far-rowed, No.	Pigs Weaned per Litter, No.	Average Weight at 70 Days, Pounds	Feed Consumed per 100 Pounds of Pigs Weaned				
					Grain, Pounds	Protein Supplement, Pounds	Minerals, Pounds	Total Concentrates, Pounds	Alfalfa Hay, Pounds
Yorkshire	43	38	7.6	38.4	564.3	26.7	2.2	593.2	49.2
Chester White	43	36	6.6	39.4	633.0	33.0	3.5	669.5	69.3
Yorkshire X Chester White	31	29	7.4	42.7	546.1	27.8	3.9	577.7	83.5
Chester White X Yorkshire	32	29	8.0	42.8	515.3	25.6	2.0	542.9	61.5

The summary of the rates of gain and feeds consumed per 100 pounds of gain from weaning until finished for market is presented in Table XXXII.

Both crossbred groups had a slight advantage over the Yorkshire which had lower feed requirements per 100 pounds of gain than the Chester Whites. If, however, it is taken into account that the Yorkshires were weighed out of the trial at about 20 pounds lower weight than the crossbreds, the advantage in efficiency of the crossbreds is increased materially because, as the animal's weight increases, gains become more expensive.

Hutton and Russell make the following statements regarding their results:

The Yorkshire and Chester White sows producing crossbred pigs weaned more pigs per litter than sows of the same breeds producing purebred pigs, and the crossbred pigs were significantly heavier at weaning than the purebreds.

TABLE XXXII. A SUMMARY OF THE GAINS AND FEED CONSUMPTION IN THE U.S.D.A. EXPERIMENT

(From Hutton and Russell, *U.S.D.A. Cir. 532*)

Breed	No. of Hogs	Average Weight		Average Gain		Feed Consumed per 100 Pounds Gain			
		Initial, Pounds	Final, Pounds	Total, Pounds	Daily, Pounds	Grain, Pounds	Tank-age, Pounds	Mineral, Pounds	Total, Pounds
Yorkshire	235	40.1	176.5	136.4	1.21	362.4	11.2	1.2	374.8
Chester White	136	42.5	191.2	148.7	1.30	383.9	17.1	1.8	402.7
Yorkshire × Chester White	229	44.9	197.5	152.6	1.35	357.8	11.9	1.3	371.0
Chester White × Yorkshire	247	45.3	195.3	150.0	1.33	358.6	10.6	1.1	370.3

In the experimental fattening trials, the crossbred pigs made somewhat faster and more economical gains than the purebred pigs.

The largest percentage of carcasses suitable for conversion into Wiltshire sides was from the groups produced by Chester White dams mated to Yorkshire boars.

Although less desirable than the crossbreds, the purebred Yorkshire and Chester Whites yielded a considerable percentage of carcasses satisfactory for Wiltshire side.

Other Studies of Crossbreeding Swine. Hammond (1922) in a study of hogs at the Smithfield Livestock Show in England reported advantages in favor of the crossbreds.

Callsen (1931) in a report on four swine-feeding experiments in Germany reported that the best feeding and fattening qualities were obtained from the healthy crossbred animal.

Whetham (1935) made a rather thorough study of the records of the Smithfield Livestock Show for the years 1914 to 1933. The records showed that at a weight of 60 pounds the purebreds were slightly younger but at the heavier weights the crossbreds were younger. It was found in a study of the records of 1924 to 1936 that the crossbreds gained an average of 1.28 pounds per day and the purebreds 1.21 pounds.

Shaw and MacEwan (1936) reported an average weaning weight for 91 purebreds of 35.7 pounds in contrast to 39.4 pounds for 700 crossbreds. In feeding trials 77 purebreds gained

an average of 1.15 pounds per day in contrast to 1.24 pounds per day for 325 crossbreds. The feed requirements per 100 pounds of gain were 440 pounds for the purebreds and 429 pounds for the crossbreds.

Robison (1948) reported crossbreeding results from Ohio that are in accord with the findings at Minnesota and Iowa. Three types of pigs were produced (a) purebred, (b) first cross, and (c) three-breed cross. At 8 weeks of age, the three types of litters, out of gilts, averaged 193.5, 187.5, and 240.7 pounds, respectively. Litters out of sows at 8 weeks averaged 229.8, 259.1, and 246.0 pounds, respectively. Two groups of three-breed crossbred pigs reached a 220-pound market weight 10 and 13 days earlier than the purebred Duroc check lot pigs and required less feed per unit of gain.

Headley (1940) conducted four experiments with crossbred pigs in contrast to purebreds and concluded that “. . . the crossbred Duroc-Poland China pigs made significantly greater and more economical gains than the purebred Duroc pigs.”

The Illinois Study of Crossbreeding Swine. Carroll and Roberts (1942) reworked the data of previous studies on crossbreeding swine and concluded: “These averages do not support the belief that hybrid vigor can be expected in the majority of crosses between breeds of swine.”

They re-examined each of the experiments reported by others according to the following standard: “For crossbreds to be judged beneficial, the performance of the crossbreds must excel the performance of the better of the two parental strains of purebreds.”

The above is in keeping with the definition of hybrid vigor or heterosis reported by Lambert (1941) as chairman of the Committee on Investigations of the American Society of Animal Production. The definition is: “Heterosis (or Hybrid Vigor). The superiority over the better parent that is exhibited by the progeny. This applies to the progeny from the crossing of strains, varieties, breeds or species.”

Lambert's definition and Carroll and Roberts' standard of appraising hybrid vigor are satisfactory where it is possible to make an over-all measure of vigor. The crossbred should show more vigor than the most vigorous parent if it is to be considered an exhibit of hybrid vigor. Unfortunately it is seldom possible to obtain a satisfactory over-all measure of vigor. When

vigor is broken down into its various components, the above definitions become defective. This point is shown clearly in Powers' study of hybrid vigor in the tomato (page 244).

The above point is amplified in the following illustration. Five major factors affect productivity or vigor as measured in commercial swine production; they are fertility, survival, rate of gain, economy of gain, and merit of the finished product. For illustrative purposes we shall assume a cross between breeds *A* and *B* with the indicated values for each of the traits contributing toward productivity:

Factor	BREED GROUP		
	<i>A</i>	<i>B</i>	<i>AB</i>
Fertility	80	60	78
Survival	60	80	76
Rate of gain	85	70	82
Economy of gain	92	82	90
Merit of product	70	85	84
Average	77	75	82

From the above and from Powers' results (page 244) it is perfectly clear that the standard of measure used by Carroll and Roberts was in error. The above values led Carroll and Roberts into an even more serious error in analyzing their data. If, in two crosses of the same breeds, breed *A* is high in rate of gain in one cross the crossbreds are compared to breed *A*, but if, in the second cross, breed *B* is high the crossbreds are compared to breed *B*. One example will illustrate the point. In Table 5, *Illinois Bulletin* 489, the following data are taken apparently from Roberts and Carroll (1939):

DAILY GAIN (POUNDS)		
Faster-Gaining Pure Breed	Slower-Gaining Pure Breed	Crossbreeds
1.50	1.45	1.58
1.79	1.62	1.79

From Roberts and Carroll's 1939 publication we learn that in one case the Poland China was the faster-gaining breed with an average daily gain of 1.50 pounds, and in the second case the Duroc made the faster gains (1.79).

The above method of analysis is somewhat akin to that of the golfer who plays two balls but counts only his better ball on

each hole. The farmer cannot operate that way. He has the choice of a breed or a crossing program. He cannot take the Duroc one year because its rate of gain is high and the Poland China the next because its rate of gain is high. To use a sportsman's expression, "he must call his shots before he makes them." Furthermore the only way the livestock producer can get the high fertility of one breed, the rapid and economical gains of a second, and the quality of carcass of a third is to use a crossbreeding program.

Crossbreeding Beef Cattle. The crossing of the beef breeds for the production of market animals has been a common practice in Great Britain for a long time. It has been practiced to a limited extent in this country. Shaw and MacEwan (1938) reported on a study of crosses of Shorthorn \times Aberdeen-Angus, Shorthorn \times Hereford, Shorthorn \times Galloway, Aberdeen-Angus \times Hereford, Aberdeen-Angus \times Galloway, and Hereford \times Galloway. In their study, for each cross cows of both breeds were crossed with bulls of the opposite breed, and purebred animals of all four breeds were used as controls. Their results showed definite advantages in the crossbreds over their purebred relatives in rate of gain and in quality of carcass.

TABLE XXXIII. SUMMARY RATES OF GAIN WHILE ON FEED AND QUALITY OF CARCASS PRODUCED BY BEEF CATTLE OF DIFFERENT BREEDING

(From Shaw and MacEwan, *Sci. Agric.*)

Breeding	Average Daily Gain when on Feed, Pounds	Percentage of Top Grade Carcass
1. Shorthorn-Aberdeen-Angus	1.82	86.4
2. Hereford-Shorthorn	1.73	84.4
3. Hereford	1.67	84.0
4. Aberdeen-Angus	1.72	75.7
5. Aberdeen-Angus-Hereford	1.72	67.8
6. Hereford-Galloway	1.73	66.6
7. Shorthorn	1.77	65.2
8. Shorthorn-Galloway	1.77	61.7
9. Aberdeen-Angus-Galloway	1.69	45.7
10. Galloway	1.61	14.0

Phillips, Black, Knapp, and Clark (1942) reported on the comparative results of high grade Hereford steers and crossbred

steers out of Hereford females and by Shorthorn bulls. As a study of hybrid vigor the experimental procedure was obviously faulty, but if the problems of the western beef producer are taken into account the plan is satisfactory. Grade Hereford cattle predominate in the West; a breeding problem the rancher then has to face is whether he shall continue to raise grade Herefords or cross to some other breed or breeds. A summary of the data on the results of the first two crops of steers is presented in Table XXXIV.

TABLE XXXIV. A SUMMARY OF DATA ON PUREBRED AND CROSSBRED STEERS

(From Phillips, Black, Knapp and Clark, *Jr. An. Sci.*)

Items Compared	1939-1940		1940-1941	
	Purebred	Crossbred	Purebred	Crossbred
Number of steers	29	23	38	34
Birth weight	79.5	83.2	79.1	84.8
Age at weaning	181.8	184.5	180.3	174.7
Weaning weight	402.6	429.1	402.6	416.8
Final feed-lot weight	875.4	927.6	883.5	968.3
Feed-lot gain	472.8	498.5	480.9	551.5
Daily gain in feed lot	1.68	1.77	1.81	2.08
Sales weight	853.8	902.8	850.8	927.6
Cold carcass weight	500.2	536.8	497.6	558.8
Dressing per cent	57.1	57.9	56.3	57.7
Slaughter steer	16.8	16.7	16.0	15.6
Carcass grade	16.6	14.4	15.9	15.5
Cost of feed per 100 pounds gain	7.16	7.12	8.28	8.18
Sales price per hundredweight	10.50	10.34	11.58	11.64
Sales value per steer	89.37	93.33	98.57	107.92
Total cost of feed and marketing	40.20	42.44	47.12	53.08
Returns per steer	49.17	50.89	51.35	54.84

It is to be noted that the crossbreds excelled the purebreds in all respects except slaughter steer grade, carcass grade, and sales price. The average feed-lot weight of both groups of crossbreds

was considerably heavier than the purebreds'. If this factor had been taken into account crossbreds would show to still better advantage in feed cost per 100 pounds of gain and, at the same slaughter weight, the carcass grades might have differed.

One of the most interesting points, and one of considerable importance, is that the crossbred steers had definitely less digestive disorders than the purebreds (Table XXXV).

TABLE XXXV. PERCENTAGE OF STEER DAYS IN WHICH DIGESTIVE DISORDERS OCCURRED

(From Phillips, Black, Knapp and Clark, *Jr. An. Sci.*)

Items Compared	1939-1940			1940-1941		
	Purebred	Crossbred	Difference	Purebred	Crossbred	Difference
Total steer days	8,149	6,463	10,070	9,010
Per cent of steer days with steers bloating	0.82	0.09	0.73 *	2.99	1.31	1.68 *
Per cent of steer days with steers off feed	0.34	0.74	0.40 *	0.07	0.04	0.03
Per cent of steer days with steers scouring	0.15	0.11	0.04	1.10	1.05	0.05
Per cent of steer days with digestive disorders	1.31	0.94	0.37 †	4.16	1.75 *	

* P 0.01. † P 0.05.

Baker and Quisenberry (1944) report the comparative results on the heifers produced in the above experiment but developed as breeding animals (Table XXXVI). The data on the heifers contain more evidence of increased vigor than those on the steers. The crossbreds were heavier at birth, and at 18 and 30 months. Furthermore, the crossbreds scored higher on body conformation.

Since, for this trial, data are not available on the straight Shorthorns we are not justified in ascribing the increase to heterosis. As far as the western cattleman is concerned that is of no consequence. He wishes to know: "Is it advisable for me to raise high-grade Herefords or to cross?" Heterosis and the means by which it is accomplished are fundamental problems, but the farmer's and the rancher's questions regarding procedure require economic answers as well as biological ones.

TABLE XXXVI. COMPARISON OF GROWTH BETWEEN HEREFORD
AND HEREFORD × SHORTHORN HEIFERS
(From Baker and Quisenberry, *Jr. An. Sci.*)

Breed	Hereford			Hereford × Shorthorn		
Year born	1939	1940	mean	1939	1940	mean
Number of sires used	2	3		2	2	
Number of heifers at 30 mo.	21	34		23	30	
Average birth weight, lb.	76.7	72.4	74.1	77.0	77.1	77.1
Average weaning weight, lb.	388.8	384.7	386.3	390.7	395.7	393.5
Average days weaned	178.1	185.3	182.5	175.9	177.5	176.8
Weaning weight corrected for age at weaning, lb.			379.9			400.1
Average gain birth to weaning, per cent	312.1	312.3	312.2	313.7	318.5	316.4
Gain birth to weaning corrected for age, per cent			305.5			323.4
Average weight at 18 mo., per cent	737.9	717.9	725.5	765.8	784.6	776.4
Average weight at 30 mo., per cent	1,090.8	1,024.4	1,049.7	1,163.4	1,118.0	1,137.7
Average gain weaning to 30 mo., per cent	702.1	639.7	663.5	772.7	722.3	744.2
Average body score yearling, per cent	69.6	72.9	71.6	73.6	77.1	75.6

Crossing Beef Cattle for Adverse Climates. Rhoad (1938) reported some interesting and valuable information on crosses between the Aberdeen-Angus and Brahman cattle. The pure Aberdeen-Angus and three-quarter-bred Aberdeen-Angus were influenced more by high atmospheric temperatures than the pure Brahman or halfbreds. The first two groups showed a greater respiration rate per minute and a higher body temperature. The greater heat efficiency of the Brahman showed partial dominance.

A study of the grazing habits showed that the Aberdeen-Angus and three-quarter-bred Aberdeen-Angus utilized less total time in grazing but grazed more frequently than the halfbreds and full Brahman.

The high atmospheric temperature did not influence the rumination of the purebred and halfbred Brahman, but the purebred and three-quarter-bred Aberdeen-Angus often ceased ruminating when the temperature became very high.

Rhoad and Black (1943) made a study of hybrid beef cattle for the Gulf Coast region. The Brahman was crossed with

Angus, Shorthorn, and Hereford. The authors state, "Hybrid cattle with one-fourth to one-half blood of a Brahman breed and the remainder from a British breed have demonstrated unusual ability to produce beef from grass." The crossbreds were superior to the straight Brahman in carcass quality and to the British breeds in ability to resist the high humidity and temperatures.

In the above-mentioned studies it was demonstrated that the hybrids were inferior to one of the parental breeds in most characteristics, yet, as an animal suited to the Gulf Coast region, the hybrids were distinctly superior to both. It is not unlikely that other wide crosses might produce hybrids better suited to special regions and climatic conditions.

Crossbreeding Sheep. Miller (1935) conducted a crossbreeding trial with sheep on much the same basis as the United States Department of Agriculture conducted their trial with beef cattle. Rambouillet ewes are generally recognized as the basic sheep for the western range.

One portion of the experiment was a comparison of the merits of Rambouillet ewes with Romney-Rambouillet crossbreds. The second portion was to determine the best type or breed of ram to be used for crossbreeding.

For their range conditions the crossbred ewes were less satisfactory than the Rambouillet. The Rambouillet ewes bred earlier in the season (an average of 21 days), a distinct advantage under their range conditions. The Rambouillet ewes had a higher percentage of twins. The death loss was higher among the lambs out of Rambouillet ewes, but they still averaged more lambs raised.

Hampshire, Suffolk, Shropshire, and Southdown rams were crossed with both types of ewes, and also the Romney and Rambouillet were used on Rambouillet ewes. A summary of production records by rams used is presented in Table XXXVII. The lambs out of the crossbred ewes were handicapped by being younger when taken off trial. Under circumstances in which it was not essential to have early lambs, the results would probably have been somewhat reversed, because their daily gains were higher.

Of sires Miller states, "Sires of the larger breeds, namely, the Hampshire and Suffolk, produce lambs weighing from 6 to 8

TABLE XXXVII. WEIGHT, AGE, DAILY GAIN, AND VALUE PER LAMB;
POUNDS OF LAMB PRODUCED PER EWE

(From Miller, *Calif. Bul.* 598)

	Num- ber of Lambs	Average Weight of Lambs, Pounds		Average Age Lamb, Days	Average Daily Gain, Pounds	Pounds Lamb per Ewe	Ap- praised Value per Lamb
		Birth	Final				
Group A, Rambouillet Ewes, Six-Year Average							
Hampshire	144	10.6 ± 0.11	77.0 ± 0.68	121.0	0.548	99.0	6.71
Suffolk	138	10.4 ± 0.10	78.3 ± 0.76	120.3	0.564	96.5	6.51
Shropshire	135	9.8 ± 0.10	72.9 ± 0.67	116.8	0.540	87.9	6.46
Southdown	141	9.5 ± 0.11	70.4 ± 0.67	118.1	0.515	88.7	6.00
Romney	89	9.6 ± 0.13	70.0 ± 0.84	115.0	0.525	84.2	0.00
Rambouillet	146	9.6 ± 0.10	70.7 ± 0.62	119.9	0.509	92.1	5.52
Group B, Romney-Rambouillet Ewes, Four-Year Average							
Hampshire	96	10.6 ± 0.17	69.5 ± 0.92	95.8	0.615	83.5	5.91
Suffolk	100	10.3 ± 0.13	69.2 ± 0.85	96.2	0.612	87.6	6.17
Shropshire	103	9.4 ± 0.11	62.6 ± 0.91	94.4	0.563	80.6	5.06
Southdown	102	9.1 ± 0.13	60.4 ± 0.67	92.4	0.555	77.0	5.36

pounds more at 3½ to 4 months of age than sires of the smaller breeds such as the Shropshire and Southdown." He is in accord with Winters *et al.* (1946): "The effects of crossbreeding on productivity were most favorable when rams of the larger breeds were used."

In the final sale of the California lambs the carcasses of the Southdown and Shropshire crosses brought a somewhat higher price than the Hampshire and Suffolk crosses. In final returns per carcass the ranking was Hampshire, Suffolk, Shropshire, Southdown, and Rambouillet on the Rambouillet ewes. The ranking of rams on the crossbred ewes was the same except that the Southdown surpassed the Shropshire.

Winters *et al.* (1946) made a study of methods of appraising productivity in sheep. The productivity of Shropshire ewes was increased an average of 12 per cent by breeding to Hampshire and Columbia rams. The productivity of grade Rambouillet ewes was increased 14 per cent by mating them to Leicester and Hampshire rams in contrast to rams of the smaller Cheviot breed.

The above results indicate again that all the benefits of crossbreeding may not arise from hybrid vigor, at least in the more common understanding of that term.

Crossbreeding Dairy Cattle. Reed (1946) reported marked increased production in dairy cows as the result of crossbreeding. The crosses made were:

Red Dane × Guernsey
 Holstein × Jersey
 Jersey × Holstein
 Jersey × Guernsey
 Red Dane × Jersey
 Holstein × Guernsey
 Jersey × (Red Dane × Holstein)
 Holstein × (Red Dane × Jersey)

The summarized results of the study are given in Table XXXVIII.

TABLE XXXVIII. DAIRY PRODUCTION OF PARENTAL STOCK AND THEIR CROSSBRED DAUGHTERS

(Data from Reed, *Country Gentleman*)

Breeding	Milk, Pounds	Butterfat	
		Per Cent	Pounds
Purebred	10,416	4.53	453
Crossbred	13,095	4.62	599
Increase	2,579	0.09	146
	25%	2	32

Proved sires were used in Reed's study; he mentions one animal in particular whose daughters of his own breed had an increase of 43 pounds of butterfat but whose crossbred daughters had an increase of 220 pounds over their dams. The whole experiment shows a rather unusual increase in production as the result of crossing breeds. This, however, is not surprising because at least some of the dairy breeds have been kept separated for a long time and they possess many differences in superficial characteristics. Both of the above provide possibility for genetic differences in production, and hybrid vigor is dependent on genetic differences.

Crossbred Poultry. In a rather comprehensive study of crossbred poultry, Warren (1927 and 1930) found that in general

crossbreds were superior to purebreds. The Singlecomb White Leghorn-Jersey Black Giant crossbreds were superior to the two purebreds in all measurements of vigor. The Singlecomb White Leghorn-Singlecomb Rhode Island Red crossbreds were in general superior to the purebreds, but in a few respects the crossbreds only equaled the superior of the two breeds involved. In chick mortality and rate of growth, both the crosses of Singlecomb White Leghorns by Barred Plymouth Rocks and of Singlecomb Rhode Island Reds by Barred Plymouth Rocks were superior to the purebreds.

The average egg production of the White Leghorn was about 175 per year, that of the Black Giant about 160, and of the crossbreed of the two about 200. In a cross of the White Leghorn with the Rhode Island Red the production of the purebreds was given as about 212 and 169, respectively, with 215 for the cross of Leghorn male on Rhode Island Red females and 197 for the reciprocal cross.

Strains within the White Leghorn breed also were crossed. The average winter egg production for the two strains was 79, and the average for the two types of crosses was 90.5.

As a result of his studies Warren states:

To the average poultry breeder it may appear inconsistent to suggest the practice of crossbreeding after years of proclaiming the gospel of pure breeding. The use of the pure or standard-bred fowl was urged because it had been improved by skilled breeders and made a more productive and uniform market animal, and when comparing the pure bred and the mongrel all these advantages exist. However, the hybrid fowl, except for color in a few crosses, is more uniform than most standard breeds and in vigor and productiveness it is superior to the breeds used in its origin. The work in plant breeding would indicate that the best results may be expected from crossing of breeds and varieties that have survived a period of breeding toward a definite standard. The utilization of the hybrid is not a reversion to the old system of promiscuous breeding, but the adoption of a system which is of value only when well-bred standard fowl are available. The poultryman, noted for his exact standards, has built up breeds and varieties that provide favorable material for crossbreeding. If the use of crossbreds becomes widespread it will not mean the reversion to mongrelization of the fowl, but will place a premium upon well-bred pure breeds. It will have a tendency to place poultry breeding in the hands of the

specialist, since in his keeping is the material which must be used to replenish the stock of the user of crossbreds.

Mehrhof, Ward, and Moore (1945) made a study of the fattening qualities of purebred and crossbred cockerels. The crossbreds were heavier than the purebreds at 10 weeks, and, with the exception of one cross, the White Leghorn $\times F_1$ (Rhode Island Red \times Light Sussex), they were heavier at 12 weeks. In feed utilization the crossbreds resulting from Rhode Island males on Light Sussex females was most efficient. The addition of White Leghorn breeding to the Rhode Island Red, to the White Sussex, or to the cross of the two lowered the efficiency of feed utilization.

Dudley (1944) studied the effects of crossing the Rhode Island Red and White Leghorn breeds of poultry. The crossbreds had a lower mortality, reached egg production at an earlier age, and had a higher annual egg production.

Inbred Lines for Crossing. Since 1937 considerable effort has been directed to the development of definite inbred lines with the expectation that they would cross to better advantage than the so-called old standard breeds. The assumption has been that some of the less desirable genes should be eliminated by inbreeding and that, if lines with higher degrees of genetic purification are used, the results should be more consistent.

The results (Winters *et al.*, 1944; Dickerson, Lush, and Culbertson, 1946; Sierk and Winters, 1951; Chambers and Whatley, 1951; and Hetzer, Hankins, and Zeller, 1951) are encouraging as regards the possibilities of improving the production of crossbreds through the use of superior inbred lines. Dickerson, Lush, and Culbertson crossed inbred lines of Poland China hogs and obtained lower mortality in the crosses, both before and after birth until at 5 months it amounted to 42 per cent. The crosses had some advantage in weight at birth and at 21 days, but at 56 days they were 12 per cent heavier, and at 154 days 21 per cent heavier.

Winters and his associates (1944) crossed inbred lines belonging to the Poland China breed and inbred lines belonging to different breeds. The over-all estimate of vigor from these data and data from a previous study of breed crosses yielded an estimated increase in vigor as follows:

Cross	Advantage, Per Cent
Outbred breed crosses	
First cross	6.3
Back cross	7.5
Three-breed cross	11.7
Line crosses	
Within breed	10.6
Between breeds	19.9

The above data were verified in a later study by Sierk and Winters (1951); the later study was the result of the analysis of considerably more data than were included in the above. A still later and more comprehensive study by England (1952) is in accord with the above.

The results indicate, as expected, that the crossing of inbred lines belonging to different breeds may be expected to yield more hybrid vigor than lines belonging to the same breed. This is in keeping with results obtained in corn breeding by Hayes and Johnson (1939) and Johnson and Hayes (1940). Hybrid vigor is dependent on genetic diversity, and in general more genetic diversity may be expected between lines of different breeds than between lines belonging to the same breed. If this were not true, it would be necessary to conclude that the past effort put into the breeds had been a failure because there had not been sufficient genetic differentiation of the breeds to make their classification as separate breeds worth while.

Chambers and Whatley (1951) reported on crosses of inbred Duroc lines of swine. They reported that the three-line-cross litters averaged nearly 350 pounds heavier than the outbred litters at 6 months of age. The authors came to the conclusion that selected inbred lines may be used in crosses to raise the level of performance.

Hetzer, Hankins, and Zeller (1951) reported on first crosses between six inbred lines of swine developed at the United States Agricultural Research Center at Beltsville, Maryland. The inbred lines used had been developed from crossbred foundations involving seven older breeds, namely, Danish Landrace, Danish Yorkshire, English Large Black, Chester White, Duroc, Hampshire, and Poland China. They report as follows:

Crosses exceeded inbreds by 1.2 pigs per litter, or 14 per cent, at birth; by 1.7 pigs, or 27 per cent, at 21 days; and by 1.7 pigs,

or 29 per cent, at 56 days. Therefore, both prenatal and post-natal viability were higher among crosses than among inbreds. In litter weight, crosses exceeded inbreds by 2.4 pounds, or 10 per cent, at birth; by 17.9 pounds, or 28 per cent, at 21 days; and by 64 pounds, or 40 per cent, at weaning. In individual pig weight, differences in favor of crosses were 0.3 pound, or 3 per cent, at 21 days; 2.7 pounds, or 10 per cent, at 56 days; 6.6 pounds, or 8 per cent, at 98 days; and 9.3 pounds, or 6 per cent, at 140 days. Carcass data showed that crosses had a slightly higher dressing percentage, a slightly lower yield of lean cuts, and more fat than inbreds.

When the performance of the crosses was adjusted to correspond to that of crosses between non-related inbred lines, the advantages in their favor were generally higher than were indicated by the actual results. These results agree with the view held by most workers that, the lower the relationship between inbred lines, the higher, in general, is the performance of crosses between them. The results also agree with published data in that the crosses exhibited a proportionately greater advantage in litter size or viability than in rate of growth.

Characteristics of Breeds or Line for Use in Crosses. Of the two rather sharply contrasted views regarding the traits that should be possessed by lines or breeds to yield optimum results in crossing, one is that the breeds or lines should differ in their possession of economic characteristics. According to this view, a desirable cross in swine would be to cross a line relatively low in fertility and carcass quality but high in rate of gain and efficiency of gain with one that was superior in fertility and carcass quality but deficient in rate of gain and efficiency of gain, the view being that desirable genes are for the most part dominant. Therefore, bringing together breeds or lines sharply contrasted in the possession of desirable characteristics would result in each complementing the other and the crossbreds tending to possess the desirable traits of both parents. This view is developed largely around confidence in the dominance of desirable genes and traits over undesirable.

Weaknesses in the above view are: First, it may be too difficult and expensive to maintain breeds or lines that are markedly deficient in any one economic trait. A breed or line that is definitely weak in any one of the major economic characteristics be-

comes a very difficult and expensive stock to maintain. The point at which the benefits from crossing are not sufficient to offset the expense of line maintenance can easily be reached. A second weakness in the above theory is that it rests upon the assumption that the dominance of desirable genes and characteristics is the major point of consideration in obtaining the maximum desirability in crosses. This may or may not be true. It is, however, perfectly clear that additive genetic effects and genic interaction are of considerable importance. To completely separate the effects of dominance, additive gene effects, and genic interaction is difficult, if not impossible. Nevertheless, the above theory lays major emphasis on the possession of blocks of dominant genes affecting desirability.

The second theory is that maximum desirability in crosses is more likely to be achieved through the crossing of breeds or lines, each of which possesses a maximum of desirability for all traits desired in the hybrid. It needs to be recognized, however, that breeds or lines of this kind may not possess as much desirability in any one trait as is possessed by a breed or line that has been developed more specifically for one or two characteristics. On the other hand, there is scant evidence of physiological antagonisms between many desirable characteristics in farm animals. If the breeds and lines now available do not possess gene complexes that provide maximum desirability within a given line or breed (not the maximum that is to be achieved in the hybrid), then it is the job of the breeder to build up, through reorganization of the genes, gene complexes that will better achieve these ends.

A distinct advantage in the second view is that it is much cheaper and easier to maintain a breed or line well balanced in desirable characteristics than one that is markedly deficient in one or more characteristics. This is a major consideration in the practical application of crossbreeding.

The second theory contends that, if two breeds or lines possess as much of the desirable as possible in each of the economic characteristics desired but differ in superficial traits, there is reason to expect that crosses of such lines will, for the most part, prove desirable. The assumption in this theory is that genes for desirable characteristics are linked with genes affecting super-

ficial traits. In some cases the same genes may serve both purposes. It is a well-established fact that allelomorphic series of genes are to be found in all species. Some of these allelomorphs may differ, yet be of essentially equal value. Further, the genes affecting superficial traits may be expected to be linked with some genes that are outstandingly effective in stimulating desirable characteristics and others that are rather mediocre in their effects. Thus, by bringing together, for instance, a cross of black-faced sheep with white-faced sheep, different genes for growth or vigor as a whole may be linked with the white face on the one hand and with the black face on the other. The result, therefore, would be that the crossbred would obtain an increase in vigor. The view is that this type of crossing offers a greater opportunity for increased productivity than the one mentioned above. To date, the most desirable results from crossbreeding have arisen from the crossing of breeds or lines that were superior themselves and well balanced in superiority.

The author holds to the second view and is pointing his own research program toward the development of lines and breeds so that each will possess as much desirability for each economic characteristic as can be bred in them, but so that the lines will differ as much as possible in superficial traits.

General Consideration of Crossbreeding for Market Production. There is a great quantity of scientific information showing that, in general, the hybrid state is conducive to increased vigor. There are differences in hybrids, and not every hybrid is superior, but we may expect the best performance from hybrids.

The above reasoning has not been completely accepted in American livestock circles, but it has gained ground greatly during recent years. An argument frequently advanced is that nothing in livestock is comparable to the inbred lines of corn. However, Reed (1946) states:

There is some similarity between present purebred cattle and the inbred strains of corn used in producing hybrid corn. After all, the closed herd book, with registered animals tracing their lineage in a breed back to a common ancestry, and with development of the breed by selection of "top" animals, means that purebreds in the United States have become to some extent inbred strains.

The methods by which the breeds were developed has differed markedly from those by which the old lines of open-pollinated corn were propagated. The pedigreeing of livestock is admittedly not perfect but even at its worst it is far different from the situation that is general in open-pollinated corn.

The critics of crossbreeding advance two arguments: the breeds do not differ sufficiently and do not carry enough purification to make crossbreeding worth while; the breeds have been developed by painstaking care through the many years and crossbreeding will tear this down.

The two arguments are not compatible: either the breeds have been separated genetically and some degree of purity achieved or they have not. If they have been, we have a right to expect a corresponding degree of hybrid vigor when at least some of them are crossed. If, on the other hand, after all these years they have not been separated genetically and no degree of purity has been achieved, nothing has been accomplished, and there is nothing to lose. The evidence indicates, however, that something has been accomplished in the development of the breeds and that, generally, the breeds do cross to advantage. The evidence gained from crossbreeding studies is the best proof that something has been achieved in the development of the breeds.

The fear has been expressed also that crossbreeding would destroy the purebred market. If we may judge from the experience of corn breeders we have reason to expect a noticeable increased demand as the result of crossing. In swine this result has already occurred. Winters, Kiser, Jordan, and Peters (1935) stated:

The good purebred sire is the basis for the improvement of swine or any other class of commercial livestock. This is equally true of the methods of breeding swine proposed in this bulletin. Crossbreeding will not solve any difficulties nor contribute anything to constructive pork production unless good sires are used. [This is in perfect accord with Reed's 1946 report on crossing dairy cattle.] The purebred breeder has nothing to fear from the proposed methods of breeding swine. In fact, he has much to gain. Many farmers are still using grades. Farmers who follow one of the methods of crossbreeding outlined herein will utilize purebred sires in the practice; hence an increased demand for purebred sires should follow.

Wallace (1938) was thinking along similar lines when he expressed the view that in the future it would become the function

of certain purebred breeders to maintain linebred strains of swine, the combining abilities of which had been proved by tests. Thus the practical feed-lot farmer would draw continually on the purebred breeder for new breeding stock. The purebred breeder under such a system would have a far more important function to perform than he has at present.

The opinion is often voiced that the crossing of breeds does not always result in increased vigor, because the breeds lack sufficient genetic purity. This opinion maintains, therefore, that it is unwise to advocate crossbreeding. This view, however, may be countered with the query, what system of mating can be recommended that will always give satisfactory results? Every experienced stockman knows that in either grading or purebred breeding he frequently makes matings the results of which are not so satisfactory as he hoped or expected. Therefore, if in general a system of crossbreeding gives better results than the same bloodlines when not crossed, it is logical to advocate crossbreeding.

Whether crossing will be profitable or not and what system of crossing will be used will depend not only upon the amount of added vigor resulting from the cross, but also upon how the system of crossing fits into the farmer's general scheme of stock raising and management. Poultry breeding is rapidly falling into the general pattern set for the production of hybrid corn. Poultry is well adapted to this plan of procedure.

In breeding swine it is very easy for the farmer to follow continuous crossing provided that he retains only gilts for breeding. Continuous crossbreeding will also work satisfactorily if, when old sows are retained for breeding, no gilts are retained; or, if his operations are large enough to justify two boars, old sows and gilts can be used at the same time.

The sow carries her pigs about 116 days and nurses them about 56 days after birth. Thus for about 172 days the young animals are largely dependent upon their mother for nourishment and other environmental factors. This is half of a market hog's normal life. In swine the vigor added to the dam from the crossbreeding may be as important a factor as the hybrid vigor in the market animals themselves.

For sheep, cattle, and horses it is not so simple to develop a crossing system that will operate as smoothly as for hogs, be-

cause it is impossible to make a complete turnover of breeding stock in any one year. In spite of this handicap many commercial producers are working out their own schemes of rotation. The author has visited several flocks of sheep (farm as well as range) where the breeder was following a somewhat continuous crossing program. The interesting observation was that on the basis of appearance they were holding type much more uniformly than might be expected. Crossing has been worked out very successfully with sheep by many of the larger ranchers because they are able to operate, at least so far as breeding is concerned, several flocks.

Another method used successfully by many farmers is copied from British practice. The female stock is purchased and mated repeatedly to a male of a different breed until they are worn out; then a new group of females is purchased. An advantage of this system is that the turnover within the herd or flock is much greater than where females are grown out to replace aged females. A disadvantage is that this practice is an excellent means of spreading disease and parasites.

In summary it may be stated that crossbreeding is a sound method of breeding commercial livestock. It, however, is not any more foolproof than most things in life. Some crosses are better than others. One method may be best suited to a particular class of livestock and to certain economic conditions. A blueprint of recommended hybrids and varieties for certain areas, comparable to that corn breeders and horticulturists have worked out, has not been developed. Since there is so much intergradation in livestock production, it is doubtful if as systematic a scheme can be developed for livestock. There are two general rules that can be followed with a high degree of success in crossing for commercial production: (1) feed superior purified stock into the cross, and (2) keep the crosses wide genetically. The first capitalizes on additive gene effects, and the second on the dominance of linked factors and gene interaction.

New Breeds from Crossbreds. The development of new breeds from crossbred foundations is as old as the breeds themselves, for it is difficult to find a breed that does not rest on a crossbred foundation of some sort. The Arab horse is perhaps an exception but we cannot be certain even of that.

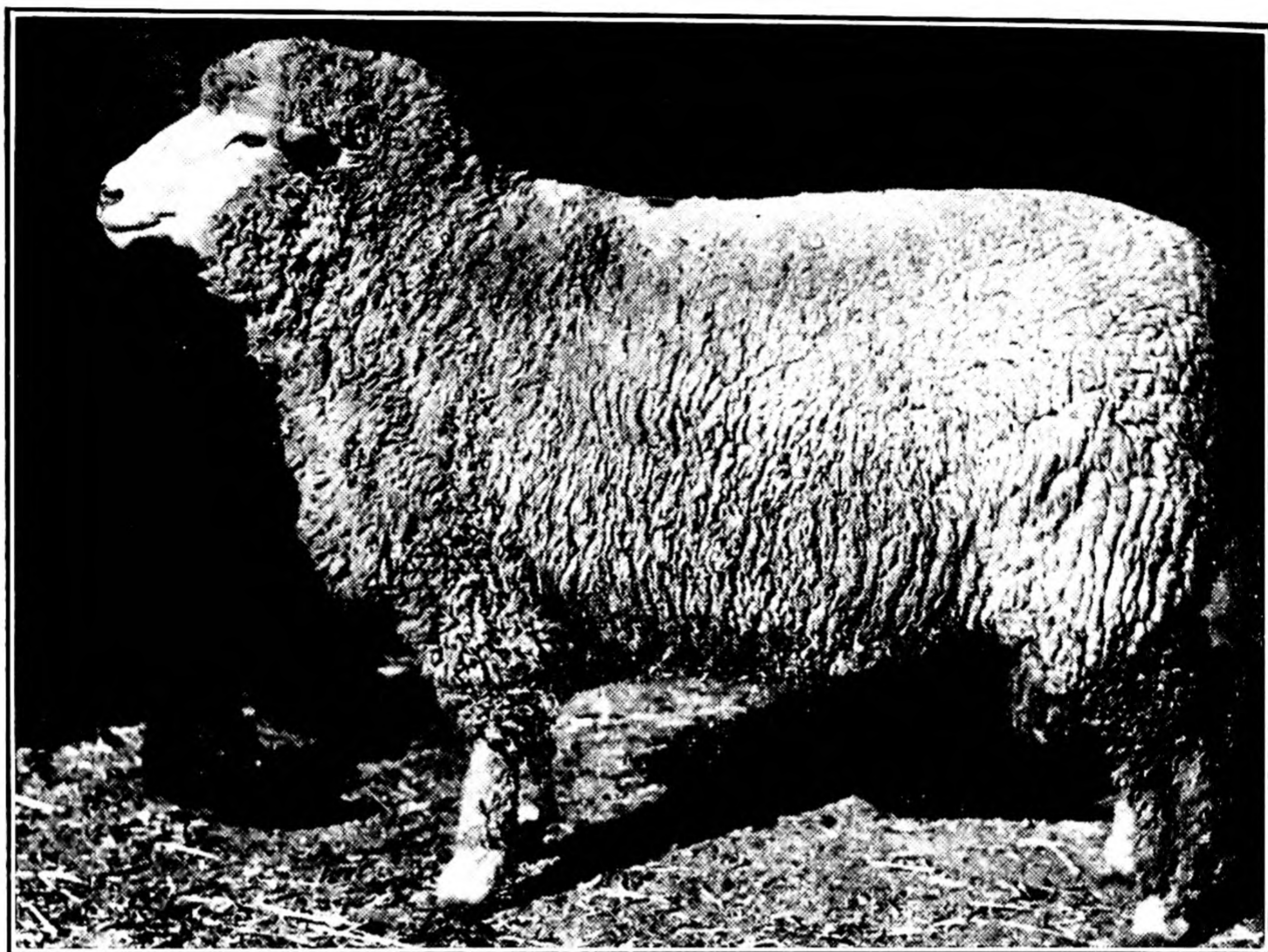


FIG. 74. A mature Columbia ram. (Courtesy U. S. Sheep Experiment Station.)

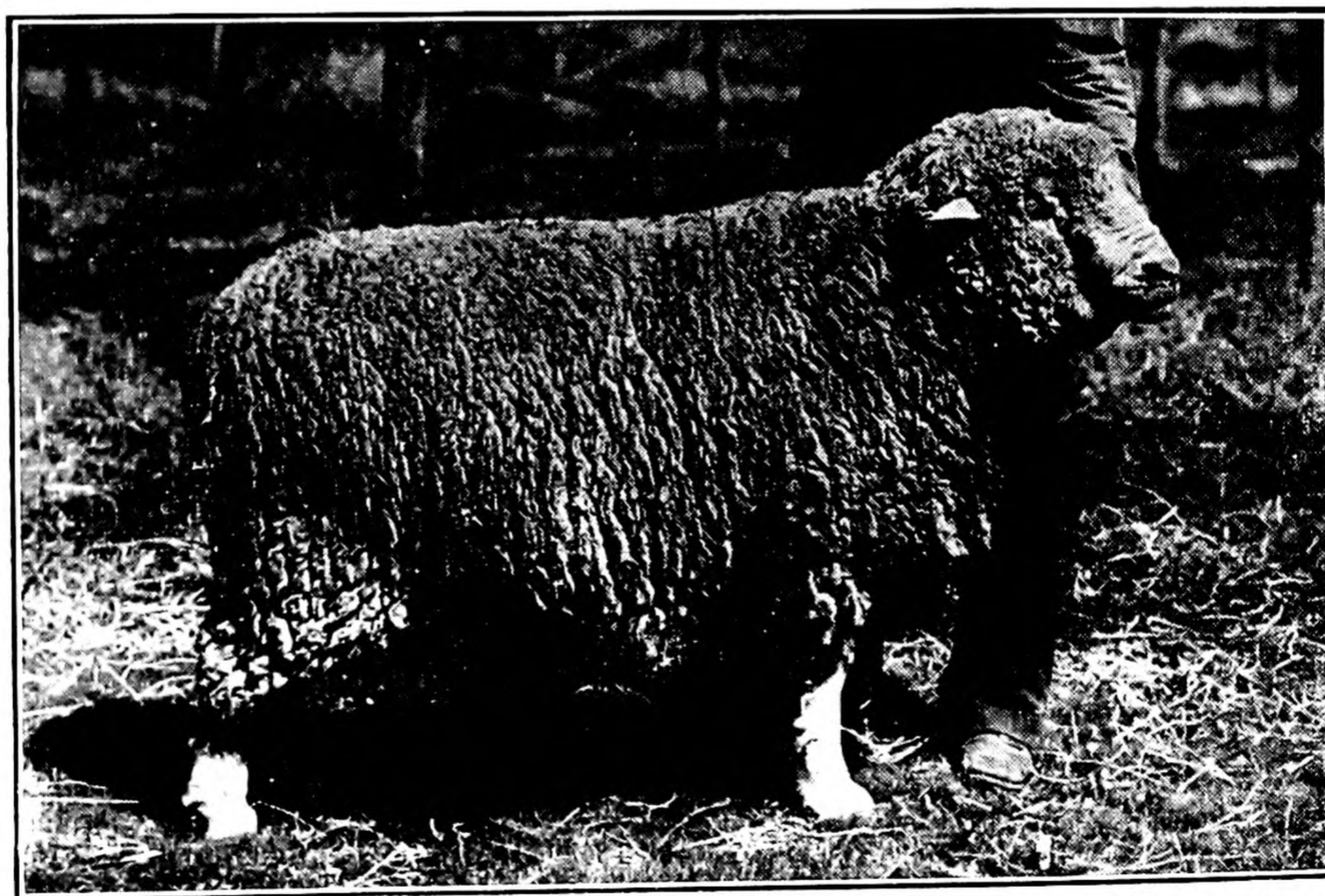


FIG. 75. A mature Targhee ram, another new breed developed by the U. S. Sheep Experiment Station, Dubois, Idaho. (Courtesy U. S. Sheep Experiment Station.)

The Oxford Down breed of sheep rests on a cross of the Cotswold, Hampshire Down, and Southdown. It was until recently looked upon as one of the young breeds, but recently the Corriedale and Columbia have been added to our breeds. The Corriedale was developed in New Zealand from a cross of Lincoln and Leicester rams on Merino ewes. The Columbia was developed by the United States Department of Agriculture from a cross of the Lincoln and the Rambouillet.

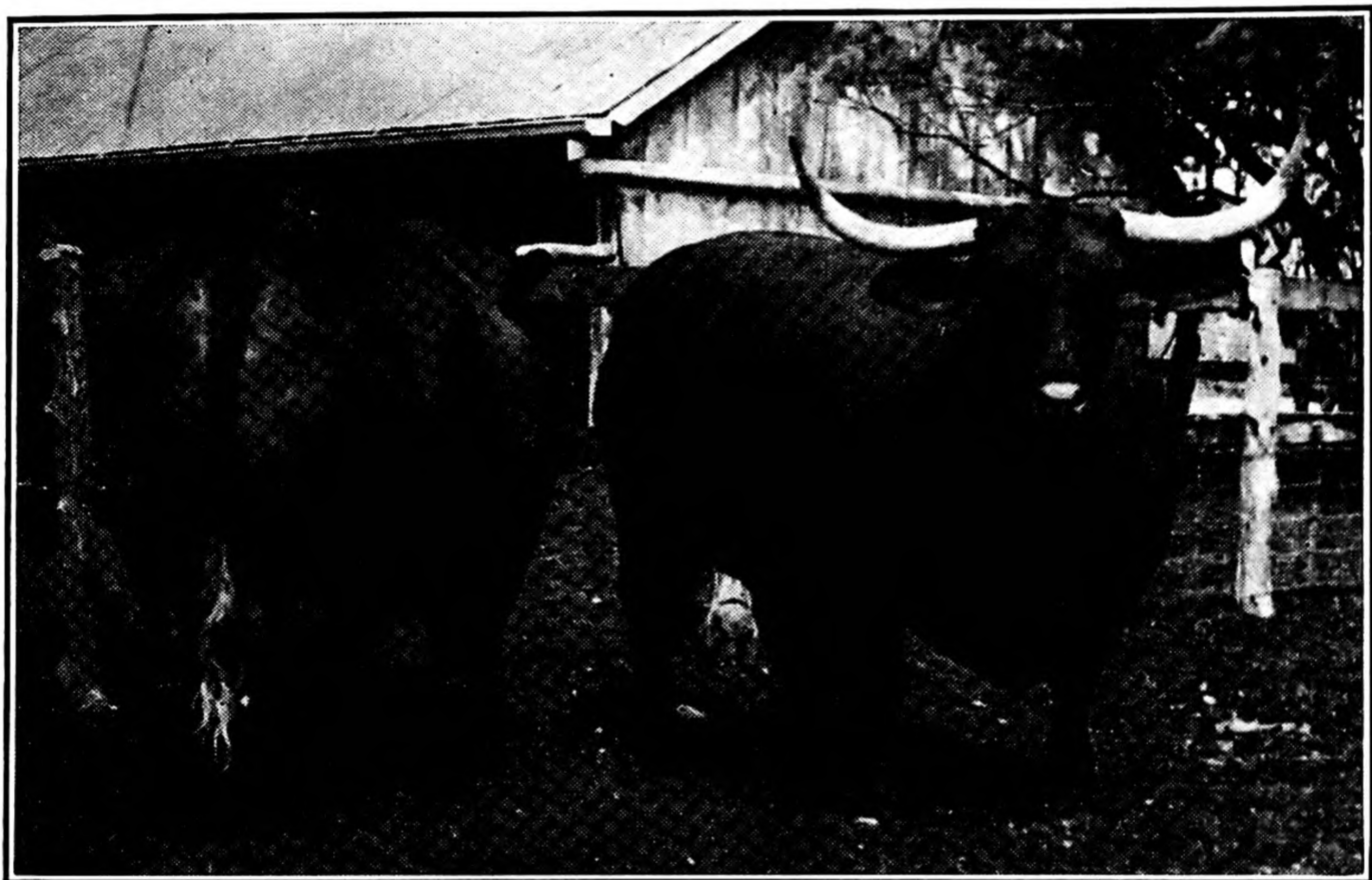


FIG. 76. Santa Gertrudis cattle. (Courtesy of King Ranch.)

The Santa Gertrudis is a relatively new breed of cattle developed by the King Ranch from the Brahman-Shorthorn cross. This new breed is cherry red, possesses lots of scale, matures rapidly, has a broad deep body, and thrives under the climatic conditions of southern United States, where the European breeds experience great difficulty.

Several new breeds of horses have been brought out during recent years (Fig. 77). Some of the breeds have come through a long process of development, and others are scarcely removed from the crossbred state. The number of years or number of generations, however, by which a breed is removed from the foundation cross is not a surer guarantee of its purity than a

man's age is a measure of his knowledge; in both the final evaluation is dependent upon what was done with the time.

Several new inbred lines of livestock (chiefly swine and sheep) have been developed; others are in the process of development. Their development is discussed in Chapter XIX.



FIG. 77. A Tennessee Walking Horse, a recently developed breed.

The fundamental reason for developing additional breeds from crossbred foundations is the opportunity for reorganizing gene associations. However, because a breed has been developed recently in that manner, there is no reason for believing it to be superior; some new gene groupings will yield inferior results. There can be no doubt, however, that the Santa Gertrudis was developed by taking some genes from the Brahman and some

from the Shorthorn and putting them into such an association that the new combination of genes served a specific purpose better than either of the old. This method of improvement appears to offer the greatest opportunity for rapid genetic change and advancement. It, after all, is only the utilization of the animal breeder's three tools—crossbreeding, inbreeding, and selection.

It has been quite generally assumed that the improvement of wild animals was accomplished primarily by selection and purification. More recent studies of population genetics indicate that wild populations through natural selection tend to develop what may be called a genetically balanced degree of heterozygosity. A rather high degree of phenotypic uniformity is achieved, and certainly some genetic purity is attained. Nevertheless, considerable heterozygosity is retained, and possibly actually attained, through the general tendency of natural selection to favor the more vigorous individuals, which possess considerable heterozygosity.

In man's early migrations, he, undoubtedly, induced many crosses unwittingly. Later many crosses were made intentionally. Both of these types of crosses led to still greater heterozygosity. It is doubtful if, during the development of the breeds, sufficient purification has resulted from selection and the breeding from within to more than slightly offset the effect of the previous crossings. In absolutely no way, of course, can the above conjecture be proved or disproved. The development of our modern breeds therefore appears to have resulted to a large extent from induced heterozygosity, which was followed by selection for type, with some breeding from within a rather large closed population. This resulted in some purification of the germ plasm, but probably, in the end, resulted in a considerable degree of balanced heterozygosity. Crossing evidence indicates, however, that, in spite of each breed's possession of considerable heterozygosity, the breeds, for the most part, differ sufficiently so that, when they are crossed, increased vigor results.

Purebred Breeding

For many years American thought regarding animal breeding has been largely dominated by the purebred philosophy. The general substance of the theory is that there are differences in purebreds but that the purebred, by virtue of being a purebred, is superior to animals bred otherwise. The theory goes even further and would have other stock replaced by purebreds if possible, otherwise by grades.

Most of the breeds were developed to fill an economic need. During the period of agricultural expansion almost any registered animal was an improvement over the common run of farm animals. Furthermore, during this expansion period, the chief need of the country in livestock improvement was more and more purebreds, especially sires. During and shortly after this phase of the livestock industry in America, the purebred philosophy of animal improvement served the needs of the industry. But with the passing of expansion, it has become increasingly important to find and develop methods of breeding focused on increased usefulness.

Producing Purebreds a Business. Usually, farmers become purebred breeders in order to make a profit. In this respect the industry does not differ materially from other industries. In an analysis of the problems of improvement, the profit motive should be kept in mind, for unless the farmer can make a profit from his purebred business there is little reason for his engaging in it. The need to make a profit from his enterprise naturally causes him to be somewhat conservative about initiating changes in his breeding and sales practices.

Methods of Breeding Purebreds. Breeders have differed widely in their methods of breeding. Some breeders have for years followed line breeding. A few have inbred rather closely, and still others have occasionally inbred and followed inbreeding

with outcrossing. But in general the popular method of breeding has been that of phenotypic selection which has been based largely on show-ring winnings. As pointed out in Chapter XII this method is not complete phenotypic selection because performance is also a part of phenotype. In dairy cattle, production records have received consideration along with the show-ring winnings but production records have too often been badly warped owing to forced records and failure to include poor records. Pedigree also has influenced selection but the estimate of a pedigree is based largely on the show-ring performance of the ancestry. In general it may be stated that the show ring has dominated breeding policy.

The argument is frequently advanced that the show ring should dominate until better methods are developed. But in too many instances those who have advanced the argument have been not only reluctant but also opposed to testing by experimentation this philosophy with newer philosophies of animal improvement. Furthermore, when experimental evidence has been presented to show other methods by which improvement can be made, the experimental evidence has been rejected too often in favor of opinion.

Ideals Set by Show Ring. The chief way in which the show ring aids in livestock improvement is by tending to keep breeders informed about what is considered correct in type.

Secondly the winning of prizes makes good advertising. Unfortunately this inducement has become the chief reason why many breeders exhibit stock.

Show Ring Often Misleading. Unfortunately the show ring is in many ways misleading. Block-type animals are overloaded with fat. Many animals become infertile as a result of the overconditioning and the unfavorable environment they live in while being prepared for the show and while on the show circuit.

A serious criticism of show standards is that they are usually arbitrary. A logical method of setting type would be according to the type that best performs the task for which it is bred. If a certain type of beef cattle is most efficient in converting feed into edible meat and at the same time produces the most valuable carcass, those qualities should determine the type desired. In like fashion, if a sow is of correct type when she reaches market weight, we should not ask that she retain those same

proportions the rest of her life. It would be more fitting to study the changes in proportions during the animal's entire growth period and to let those that are of correct type when at market weight set the type for the early and the later periods of life. There is no reason why the 600-pound sow should have the same proportions and lines as a 200-pound gilt. If the 600-pound sow was correct in type when she weighed 200 pounds and is a producer of the right kind of 200-pound progeny, then she must be the correct type even if she does not conform to the standard set; often she does not.

Some care needs to be taken in setting type even by the method suggested above, for it is possible that different lines of breeding may approach the same result by different growth patterns. The author's observations indicate such variety of approach; it would be a gross error then to attempt to make line *B* conform to the type pattern of growth made by line *A*. Probably it will be highly desirable to have lines with different patterns of growth, for different genotypes would be indicated. Different genotypes are needed if heterosis is to be obtained from crosses. Several striking examples in the history of the livestock industry illustrate serious results that followed show-ring leadership.

The insistence on the so-called roly-poly type hogs, that existed at the turn of the century, stands as a classic example of faulty leadership. This was accompanied in the case of Berkshire and Poland China with an insistence on six white points (four white feet, a white tip on the nose, and one on the tail). The insistence on the six white points disqualified or under-rated many hogs that were desirable by economic standards.

Later the so-called fence-rail type of pig was favored. The assumption was that this type of hog was more productive (it had been formerly maintained that the roly-poly type was most productive) and that this was a meat type of hog. No substantiating data were available or forthcoming, but type was changed to suit the changed fancy. The results were detrimental to the industry.

In sheep the most striking error of show-ring fancy was the demand in several breeds for a type that was wooled completely over the face and well-wooled down to the hoofs. The result was the development of sheep that became wool-blind and sheep whose legs were poorly suited to snow and mud. The final result

was that commercial producers became dissatisfied with that type of sheep.

The above-mentioned demand for sheep completely wooled over the face was in one instance accompanied by a demand for a very small ear, hidden in the wool, and a small body type. The small ear caused no particular trouble in itself, except that it handicapped desirable sheep that happened to possess a larger ear than was favored. The selection for a small type did definitely result in a handicap to the stock so developed, because practical commercial producers did not want that kind of sheep; eventually they registered their disapproval by turning to a different type.

The most recent serious economic consequences resulting from show-ring fancy has resulted from the premium paid in the show ring for the so-called pony-type of beef cattle. It appears that demand for this type is to some extent responsible for the development and spread of dwarfism in beef cattle. This is an extremely serious economic problem. Its consequences may wreck some breeding herds that represent heavy investments.

Occurrences like those mentioned above are very serious. The economic loss is heavy. Progressive livestock breeding is so slow that it takes a long time to eradicate unfortunate developments such as those mentioned above. Furthermore, once a breed loses public favor, it is extremely difficult to regain the lost popularity.

Improvement in Livestock Shows. In spite of the shortcomings of the livestock show, it has been useful, but it could be made more useful. All the market classes should be judged on hoof, slaughtered, judged on the rail, and then cut out for yield of carcass. If this were the procedure, the students of the show would have an opportunity to learn much about type. At present there is a tendency to favor animals carrying more condition than is wanted on the carcass. By following the procedure suggested, judges, as well as spectators, would learn from the show. Many times the judge simply cannot detect an animal's shortcomings. Figure 78 is a photograph of a lamb rib cut; the cut is obviously deficient in lean meat. However, the lamb from which this cut was taken appeared and felt well fleshed through the rib region. Figure 79 is a photograph of a loin cut from a hog that also appeared full in the loin. The cut,

however, shows how deficient in lean meat the hog was. Contrast Fig. 79 with Fig. 80; the differences in lean could not have been detected on the hoof by present available methods of appraising swine.

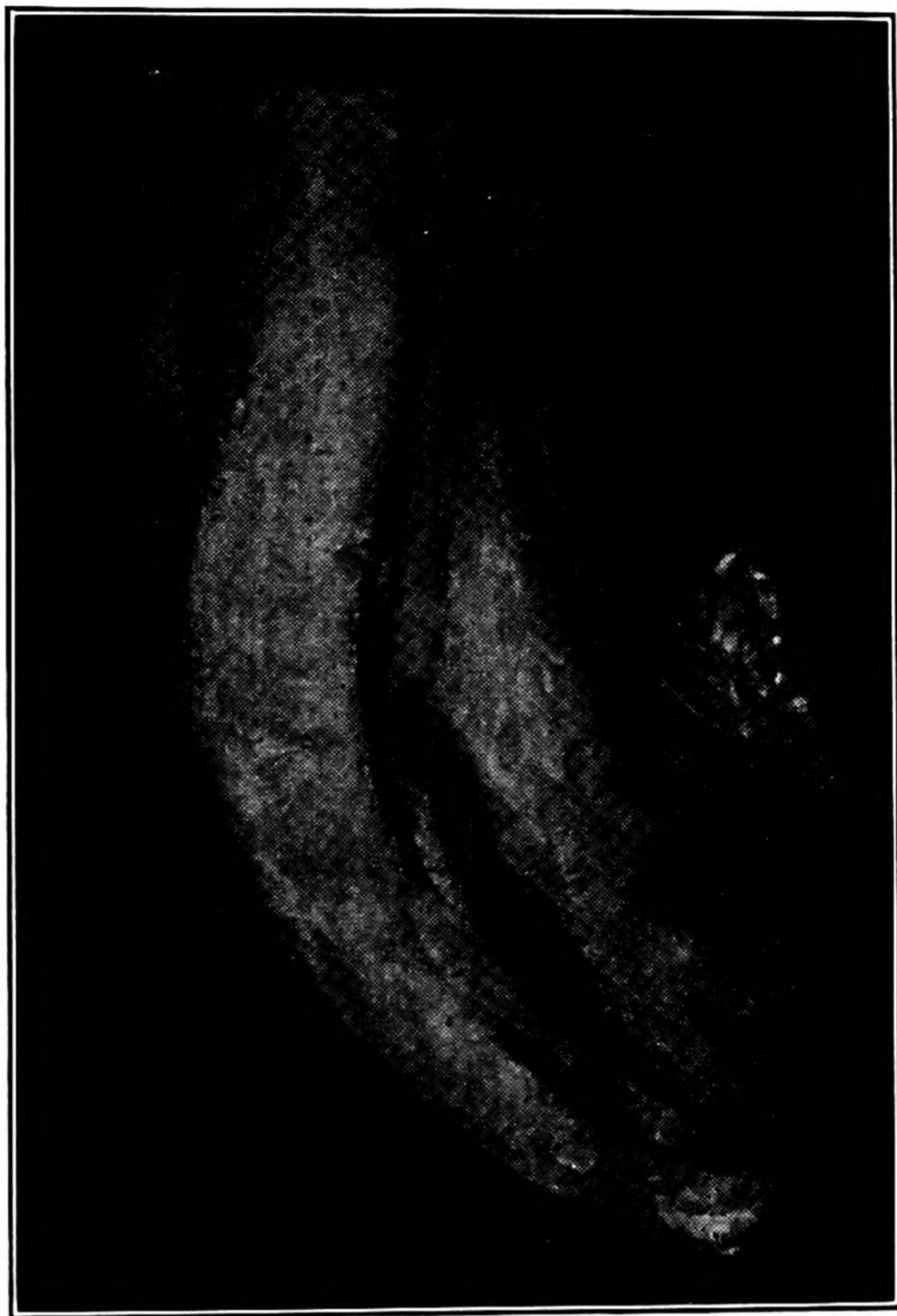


FIG. 78. A rib cut from a lamb that appeared well muscled in this region while on the hoof and whose carcass indicated superior fleshing. The cutting test revealed the lamb's shortcomings.

In the breeding classes of our large shows, in order to win it is necessary to put the animals in higher condition than is good for them. This is unfortunate. The relative fertility of many of these animals is thereby reduced. Furthermore, having the animals in so high a condition defeats the purpose of the show: the winners fail to demonstrate what breeding animals really should look like.

A further improvement in the shows would incorporate at least some record-of-performance classes. In this way the shows could exert a great influence on the improvement of our livestock. Either the show or the breed associations could supervise the



FIG. 79. A loin cut from a hog that appeared full in the loin while on the hoof and whose carcass indicated ample fullness. The cutting test revealed the deficiency.

record-of-performance work. Entrance in these classes would be dependent upon the completion of a satisfactory record-of-performance test.

About the show system Cochrane (1945) says: "Abuses of the show system would be much reduced were classes confined to animals bred by exhibitors, whose dams and maternal granddams were also bred by them, with extra marks, perhaps, for the use

of home-bred sires. We might still have breeding for shows, but it would at least be breeding, not buying."

Cochrane suggests also that dairy cattle be judged for conformation and performance on a non-competitive basis. Awards



FIG. 80. A thick loin of pork; contrast with Fig. 79. (From a Minnesota No. 2 barrow.)

of *A*, *B*, *C*, and so on, would then be given to the animal according to its individual merit rather than on the basis of competition.

Opinion is growing that the livestock show measured by annual cost has serious shortcomings. McIntyre (1946) estimates that fairs cost the American public from \$25,000,000 to \$30,000,000 annually in entrance and grandstand fees and that they cost \$5,000,000 to \$6,000,000 more, supplied by public funds.

He suggests a number of ways in which fairs might be made more educational. He would remove aged bulls from the show because they are dangerous and because there is questionable value in classifying aged bulls for type. He advocates combining the appraisal of type and production.

Eligibility for Registrations. In most breeds of livestock any animal whose sire and dam are registered is eligible for registration. In some of the breeds minor characters, such as off-color, will disqualify an animal for registration. But usually, regardless of how unsatisfactory the animal is in form or performance, it is eligible for registration as a purebred if its two parents are registered in the herdbooks of that breed. This leniency in registration makes it possible, through the occurrence of undesirable segregates, to carry in the breed many animals that are undesirable in both genotype and phenotype. In practice, however, the poorer individuals are eventually dropped from the purebred list because the breeder has nothing to gain by registering such animals.

Selective Registration. In many European countries selective registration has been practiced. According to the general plan, to be eligible for registration an animal had to pass a qualifying test. In some instances the test was merely that the animal must be satisfactory in type; in others actual performance was a part of the qualifying test.

In Germany the Württemberger breed of sheep was developed through selective registration. The standards set excluded from registration individuals that were seriously defective in either body conformation or wool. A maximum of 50 points was allowed for each, body conformation and wool, and every animal, to be eligible for registration, was required to score a minimum of 33 points in each.

The procedure of the Netherlands Herdbook Association was briefly as follows. Service certificates had to be filed soon after breeding, and birth certificates had to be filed within a few weeks after birth. Females were scored shortly after the first calf was dropped. To be eligible for registration an animal had to score 75 points out of a possible 100. Bulls were not accepted for registry unless they were from tested dams. Bulls were scored, first, soon after they were 1 year old, and again after they were 2 years old. A bull might be accepted for registration as a year-

ling but rejected as a two-year-old. The owner was then allowed 30 days in which to secure a new bull, and any services made by the rejected bull 30 days after his rejection were treated as though he were a grade. In the past about 55 per cent of the bulls presented for inspection were rejected.

In Denmark selective registration was carried to such a point that only 500 cows were registered each year. It was agreed that the registration of 500 new cows each year was sufficient to take care of the country's needs. A committee studied the applications and selected what they considered the 500 best cows. No cow was even considered until she had been in milk 3 consecutive years. Regardless of age her uncorrected fat production must have averaged more than 400 pounds per year since first freshening.

In Denmark registrations for swine were accepted only for animals bred at the state-recognized swine-breeding centers. The breeding centers were farms on which the breeders had complied with regulations. These regulations stipulated in part that the farm must each year send to the testing station half as many test litters as there were sows in its herd. Four pigs taken out of the whole litter constituted a test litter. At the testing station each litter was fed on standard rations and under standard conditions. Thus the rates and economy of gains were determined under standard conditions. After the pigs reached 200 pounds they were slaughtered and the carcasses evaluated by standardized technics.

Each breeding center was scored twice each year on management, type of breeding stock, fertility of the herd, efficiency in feed utilization of test pigs, and carcass score.

Obstacles to Selective Registration in America. In countries such as the United States and Canada selective registration presents economic problems not encountered in smaller countries. Selective registration, however, is not impossible; in the development of the Standardbred horse, animals not eligible for registration by birthright could become eligible by trotting a mile in 2:30 or pacing it in 2:25. The Brahman Cattle Breeders' Association and Columbia Sheep Breeders' Association both require inspection of animals before they are registered.

Since eligibility for registration by birthright has already become a widely established practice in this country, probably a

selective registration, a record of performance, within the breeds would be the preferable method of approach.

The progressive breeder, however, does not need to wait for the breed association to develop a record-of-performance standard. He can set up his own standards and develop a record of performance within his own herd or flock. The chief benefits from record-of-performance work must generate from the individual herds; hence the benefits are dependent upon the thoroughness of application by the individual breeder.

Corrective Matings. During the development of purebred breeding two general principles have become generally accepted. One is Bakewell's axiom, "Breed the best to the best," which, if strictly adhered to, leads frequently to inbreeding. The other is the attempt to make corrective matings. The plan of corrective matings is illustrated by Mr. Simpson's (of Gudgell and Simpson) selection of Anxiety 4th. The early Hereford cattle of this country were especially light in the hindquarters and, according to Mr. Simpson's own story, Anxiety 4th was purchased and imported largely because of his superiority in hindquarters. This importation is given credit for making a marked improvement in the fullness of hindquarters in Hereford cattle. Fortunately, however, Gudgell and Simpson did considerable linebreeding (some of it quite close). In this way they retained a fairly high relationship to Anxiety 4th, whereas, had they resorted to outcrossing and further corrective matings, not only would they have lost most of the relationship to Anxiety 4th but they would probably have lost also the benefits of the Anxiety 4th outcross.

Corrective mating has its place in constructive breeding. The corrective mating should be made for the specific purpose of correcting some definite defect in a herd or strain. The outcross needs to be followed by a certain amount of inbreeding; otherwise it is likely to be lost in subsequent outcrossings.

Prepotency. Prepotency has for a long time been regarded as of great importance in livestock breeding. Breeders for the most part have set great store by prepotency. To the breeder, prepotency means that both parents are not necessarily equal in determining the characteristics of the offspring; one parent is superior in influence to the other. The concept of prepotency is often extended to lines of breeding, the belief being that certain

lines or breeds are more prepotent than others. It has been assumed that prepotency is passed from generation to generation by certain lines of breeding.

Prepotency is not a myth. When two individuals are mated, one may have more influence than the other on the offspring. Some lines and breeds are more prepotent than others. Prepotency, however, cannot be passed from one generation to another, unless it is possessed by both the sires and the dams. If that is the case, then each individual mating will not exhibit the prepotency.

Prepotency is of importance to the livestock breeder. The animal possessed of superior individuality that is able to pass this superior individuality on to the offspring, even though the other parent is deficient in this desirability, is a valuable breeding animal.

Not all publicized instances of prepotency are authentic. Sires having a reputation for prepotency offer the breeder of purebred livestock a great advantage in sales. For this reason, it is good salesmanship to make the chief herd sire appear as prepotent as possible. The true picture of a sire's prepotency can be obtained only when all his get are taken into consideration, and when consideration is given to the merit of the females on which he was used. Too often a sire is given a high rating on the basis of a few outstanding offspring, and no consideration is given to the poor offspring he has sired. Too often a sire is given a high rating as a sire when used on an outstanding group of females. On the other hand, the sire used on inferior females may actually be a better sire than he appears from a superficial inspection of his record. Another factor affecting a sire's popular rating is the feed and care given his offspring. A sire used in a pampered herd, where each individual is given every opportunity of developing to full capacity, will appear more prepotent than the sire whose progeny is reared under less favorable circumstances.

Indications of Prepotency. The belief is still widespread that the good judge of livestock can recognize the prepotent animal from its phenotype. The assumed indicators are masculinity in the male and femininity in the female. Breed character as revealed by the head is also supposed to be an indicator of prepotency.

The known facts of genetics show very clearly that these are faulty assumptions. A high degree of homozygosity and the possession of a high percentage of dominant genes are the inherent qualities that will enable an animal to stamp his own characteristics on the majority of his offspring. Unfortunately, the phenotype of an animal does not necessarily reveal its genotype. Prepotency is not expected of the crossbred sire, because he is highly heterozygous, yet the crossbred sire frequently is very masculine in appearance.

To the student of genetics it is perfectly obvious that prepotency cannot be passed from generation to generation solely as the result of the influence of either the sires or the dams in the ancestry. The individual sire or dam may be very prepotent through the possession of dominant genes and genetic purity, but that individual can pass only the haploid number of chromosomes and genes to the offspring. If the individual to which the prepotent animal is mated possesses a very similar genetic constitution, the offspring should be as prepotent as its sire and dam. In this way it may appear that some sires possess this ability to "breed on and on." Actually, however, no sire can do this unless his breeding is highly concentrated and kept concentrated through inbreeding.

It is very likely, however, that masculinity and femininity may have some relationship to the animal's relative fertility. A difficulty encountered, however, is that very often breed characteristics are misinterpreted as indications of sex character. A further complication is due to the fact that masculine appearance is stimulated to some extent by the interstitial tissue. The germinal epithelium from which the germ cells arise may be destroyed by various types of treatments, and the individual may develop the outward appearances of masculinity (Fig. 81). This, however, is an environmental influence. It appears that, by and large, true masculinity and true femininity show some relationship to fertility and particularly to sex drive, but there is no reason to expect an association between possession of sex characteristics and prepotency.

The only true indication of prepotency in a sire is the merit of all his get. Some consideration, however, should be given to the merit of the females on which he is used. In like manner,

the only true index of a female's prepotency is her progeny. The larger the population of offspring, the more accurate is the index; inbred lines are an exception. If a high degree of genetic purity has been achieved, the prepotency of individuals within the line may be predicted with a high degree of accuracy on the basis of the family record. More and more definite lines of breeding are being developed and are coming to play an important part in

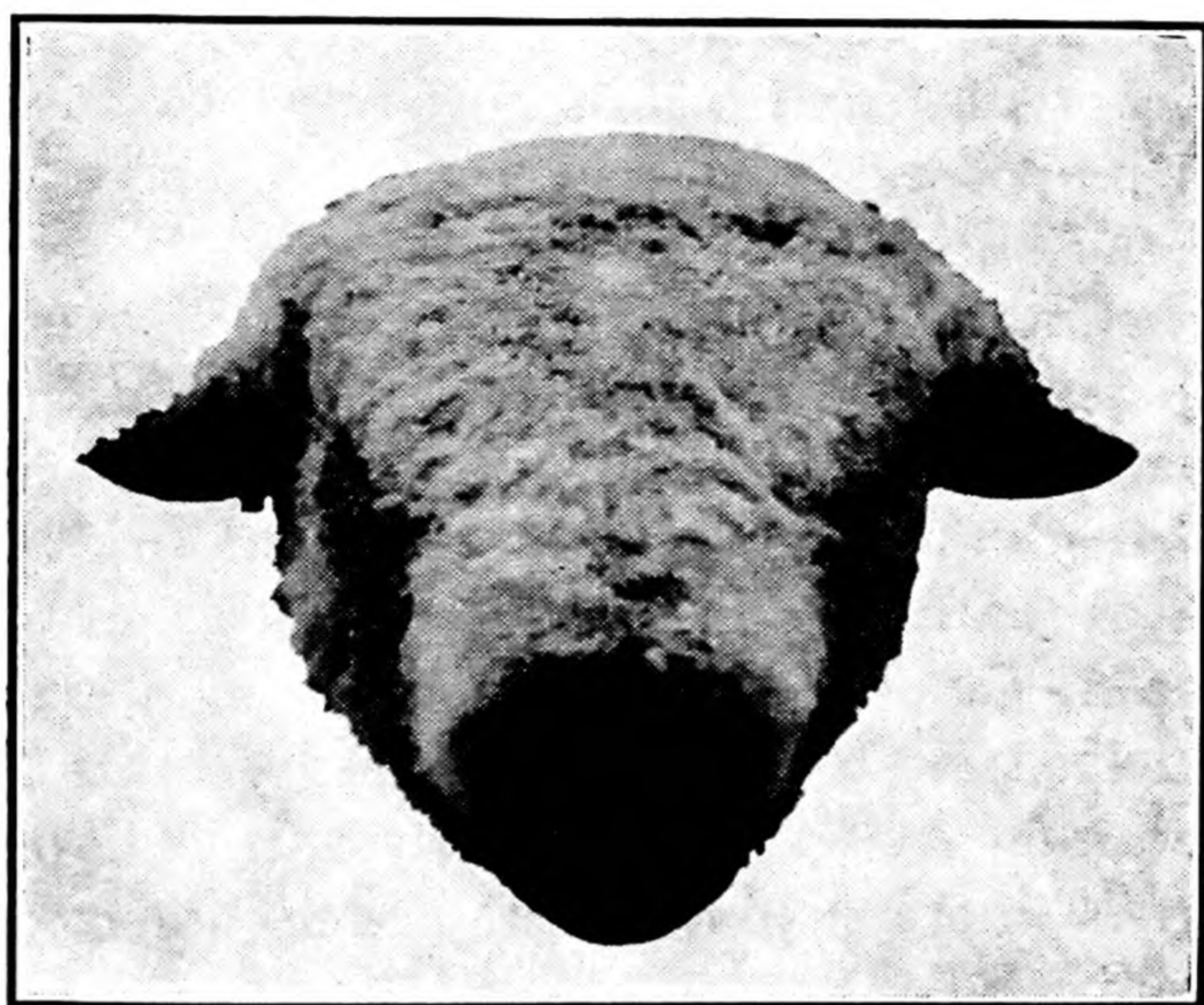


FIG. 81. This ram was sterilized by a continuous heat treatment, yet he developed considerable outward indications of masculinity and character, the assumed indicators of prepotency.

livestock breeding. This is a new situation in the breeding of farm animals, but it is rather generally accepted in plants and laboratory animals. Until such time as we have lines of known values, breeders will do well to give their attention to the proving of sires and should not attempt to read a sire's breeding index from his appearance. Breed history contains many records of great sires that gained entrance by accident to the herd in which they made their record, rather than by the owner's recognition of their greatness in advance. In like manner, breed history contains many records of animals picked to become great sires that failed to have any effect on the herd or breed.

Breed Analyses. The breeds and subdivisions of the breeds have been studied in an attempt to learn how they are constituted. Wright (1921, 1922, and 1923) set the pattern for the

best of these studies. With few exceptions these studies show that the development of the breeds has followed the same general pattern. Nearly all the present breeds rest on crossbred foundations; the breeds of more recent origin rest on crosses of the older breeds, and the older breeds rest on crosses of the then-prevailing types. In some cases the crossing continued over prolonged periods of time. Eventually the stock came to be bred from within; varying amounts of inbreeding resulted. Some of the early breeders inbred deliberately; others wandered into inbreeding. As a rule, inbreeding has remained low, most of the homozygosity achieved having come through selection rather than inbreeding.

An exception to the above is the Duchess family of Shorthorns developed by Bates and analyzed by Wright (1923). Bates drew on the Colling brothers for foundation stock. The Colling brothers had already inbred their stock considerably above the average. Bates raised the coefficient of inbreeding of the Duchess Shorthorns to about 40 per cent. The Shorthorn breed as a whole had a coefficient of inbreeding of about 26 per cent in 1920, and this figure apparently has gone only a little higher since that time. The inbreeding in the Shorthorn breed is due largely to the early work of the Colling brothers and Bates.

A summary of the estimates of the coefficients of inbreeding made on several of the breeds is given in Table XXXIX.

With the exception of the Duchess Shorthorns the amount of inbreeding for the breeds is low; although that of the Shorthorns is well above the average, it is not high. Stonaker (1943) who studied the Aberdeen-Angus breed states: "Except for a few details, the breeding systems used in the Aberdeen-Angus breed in the United States appear to be much like those in other breeds of cattle." This may be extended to all breeds so far studied, but the average interval between generations is less for sheep and swine than for cattle or horses. Stonaker found an average rise of about 0.3 per cent in inbreeding per generation in the Aberdeen-Angus, and the average interval between generations was about 5.4 years. For Hampshire sheep Carter (1940) found that the inbreeding was advancing about 0.7 to 0.9 per cent per generation. The total for the breed in the United States, however, was only 2.9 by 1935. The average interval between generations was 3.5 to 3.8 years.

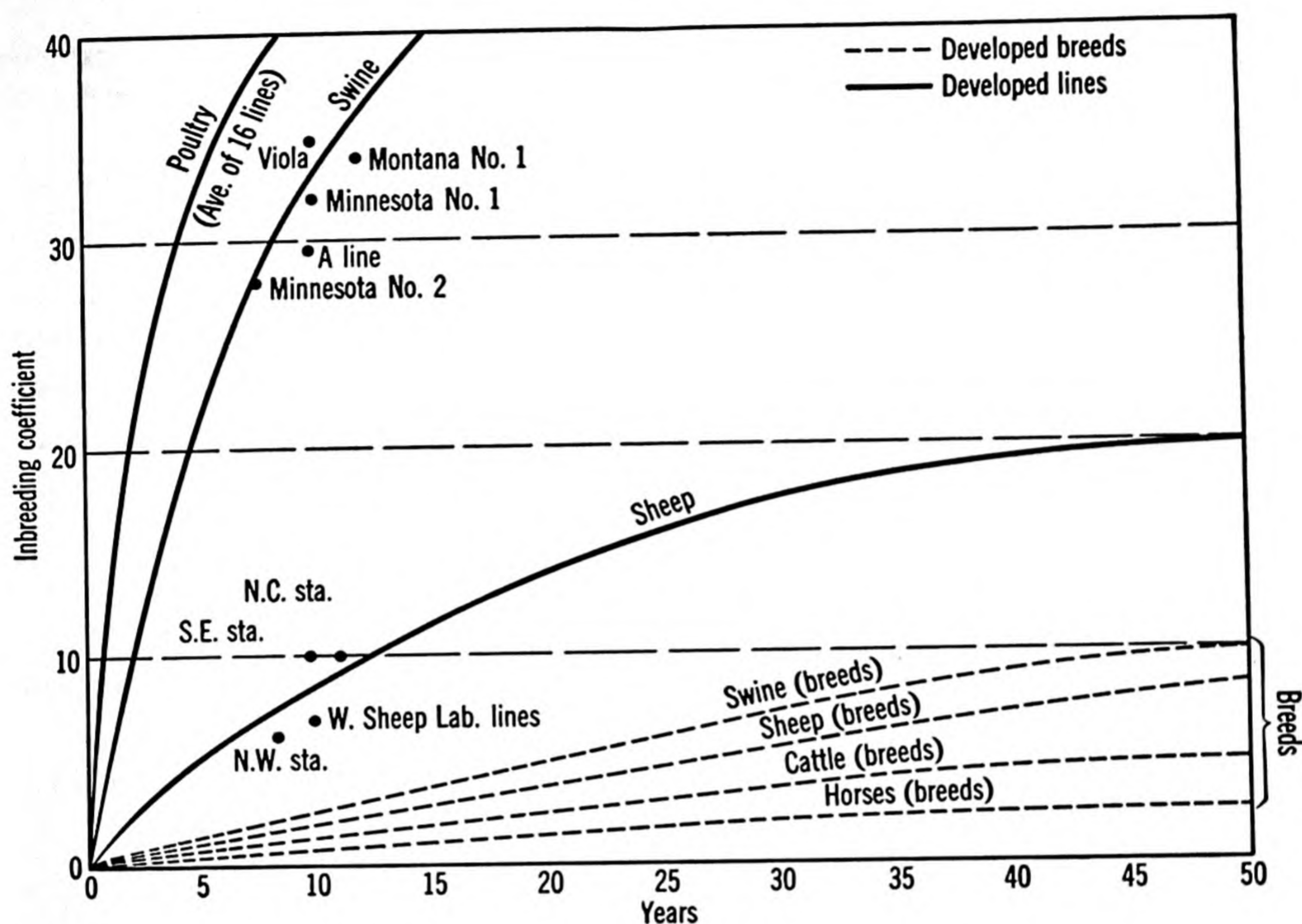
TABLE XXXIX. SUMMARY OF INBREEDING COEFFICIENTS OF BREEDS STUDIED

Breed	Date	F_x	Investigator
Shorthorn, Bates' Duchess	1810-1849	40.0	Wright
Shorthorn, Great Britain	1920	26.0	McPhee and Wright
Shorthorn, winning sires in United States	1920	25.0	McPhee and Wright
Shorthorn, United States	1920	26.0	McPhee and Wright
Clydesdale, Great Britain	1925	6.2	Smith
Rambouillet, United States	1926	5.5	Dickson and Lush
Ayrshire, Great Britain	1927	5.3	Fowler
Poland China, United States	1929	9.8	Lush and Anderson
Brown Swiss, United States	1929	3.8	Yoder and Lush
Hereford, United States	1930	8.1	Willham
Landrace, Denmark	1930	6.9	Rottensten
Holstein-Friesian, United States	1931	4.0	Lush, Holbert, and Willham
American Saddle Horse, United States	1935	3.2	Steel
Hampshire, United States	1935	2.9	Carter
Aberdeen-Angus, United States	1939	11.3	Stonaker
Standardbred Horse, United States	1940	4.4	Steel
Thoroughbred Horse, United States	1941	8.4	Steel
American Quarter Horse, United States	1941	1.7	Fletcher
American Quarter Horse, King Ranch	1941	4.89	Fletcher

These studies show that genetic purification of the breeds by inbreeding is proceeding very slowly, so slowly that it may almost be disregarded. Figure 82 illustrates the progress of inbreeding in the development of breeds of livestock and that of different inbred lines of livestock. The homozygosity that does exist must have been attained by accident and selection, especially selection for characters of non-economic importance. Some of these characters have been rather well fixed in the breeds. When coat color or type of ear becomes fixed, through linkage it automatically fixes other genes, many of which affect characters of economic importance.

One of the major purposes of breed associations and the registration of breeding animals has been the certification of the purity of the stock so recorded. As a result, the rules of most

American Purebred Associations do not allow for the introduction of genes from outside the breed. By and large, to date the purebred fraternity has frowned on all expressions of cross-breeding. In Europe most breed associations allow for the reg-



The inbreeding coefficients in 1953 for the swine lines are higher than indicated in this graph. These 1949 figures (based only on the effective breeding herd) are:

Viola line	= 43.75%
A line	= 36.75%
Minnesota No. 1	= 40%
Minnesota No. 2	= 34% (average for the N.W. herd)
M line	= 81.32%

FIG. 82. The hypothetical progress of F_w in the development of the old standard breeds and some of the more recently developed inbred lines of livestock. (From H. F. El-Issawi, Ph.D. Thesis.)

istration of animals that can show a certain number of top crosses of registered sires. In some instances, it appears that some of these so-called very short-pedigreed animals have become recorded and, when sold to buyers in the United States, are accepted as purebred stock, even by individuals who would protest recording animals with similar types of pedigrees in this country.

The Columbia Sheep Breeders' Association has made provision whereby animals that have received a sufficient number of top

crosses and meet approval in type can become recorded in the Association's stud books.

The above procedure makes it possible to increase the numbers in a breed that is too low in numbers for practical purposes to best serve the industry. It also makes it possible to introduce rather slowly some outside genes within the breed. It has been advocated by some that this should be a standard procedure for most breeds.

Another method of introducing genes within closed-breed populations has been the clandestine method of crossing, then back-crossing once or twice to the recorded breed, and recording the crossbred stock and later generations from the crossbred stock under a parentage other than its own thereby making it appear eligible for registration. In a number of cases, this procedure has resulted in definite breed improvement. It is a perfectly logical way of juggling the genes around and bringing about a genetic improvement. Unfortunately the method is and must be done illegally. A constructive method of accomplishing genetic improvement would be to allow breeders to register their intent of introducing outside genetic material and to report regularly and in detail to the Association on their procedures and results. After a time, they might then petition for registration of this stock in a special appendix of the breed's record books. The breed association could then have the records and the stock inspected by a qualified committee and approve or disapprove acceptance of the new line within the breed. This proposed method of procedure would provide an orderly, constructive, and honorable method of achieving a desired end, namely, improvement through the introduction and incorporation of genes not generally possessed within the breed being improved.

Population Genetics. Dobzhansky and his associates (1948, 1948, and 1951) and Wright and his associates (1942) have contributed a great deal of information regarding the genetics of natural populations. The fruit fly *Drosophila* has once again served a very useful purpose. The studies referred to contribute a great deal of basic information regarding natural populations. Some care must, however, be exercised as regards the application of this information to the genetics of farm animals, the genetics of human populations, and even other natural populations of animals.

Man does introduce considerable interference with natural selection in farm animals. The selection that he practices may not always be as wisely directed as it should be. Nevertheless, it does constitute an interference with what would probably have happened if natural selection had followed its natural course of events. Man also introduces an artificial environment for his domestic animals and he prohibits crossings that might occur under natural conditions.

Man, himself, on the other hand, migrates to the four corners of the earth, and, in spite of a great deal of talk of racial differences and some tendency toward racial isolationism, the history of the human race shows a great deal of racial mixing. During recent years, with the advance of medical science and the development of social science, man has come to foster the weak and to some extent handicap the strong. In other words, natural selection in the human race has been seriously handicapped.

Different species of wild animals follow different patterns of life. Some migrate great distances; others remain quite localized.

In spite of the above reservations, the studies referred to have a great deal of interest and some value in broad applications to the animal breeder. For one thing, the studies showed that lethals and semi-lethals are more prevalent in natural populations than has been generally assumed. In large samples of wild flies, from 14 to 30 per cent were found to have lethals in the third chromosome.

It appears that mutation pressures introduce a number of mutants into a population at every generation. The fate of each mutant depends upon its adaptive value and upon the genetic structure of the population in which it is released. Most mutants are unfavorable. The recessive ones accumulate in populations until they reach equilibrium values. Some mutants are deleterious when in a homozygous state, but favorable when in a heterozygous state. The mutants that produce favorable results in heterozygous populations naturally become more frequent in the population than those which are neutral when in the heterozygous state.

Many chromosomes carry genes which cannot be classified as lethals or semi-lethals, yet they reduce the viability of homozygotes. In several other portions of this book, the author has pointed out that it is his opinion that genes low in productive

effect are more serious to livestock breeders than the more destructive lethal and semi-lethal genes for the reason that the latter can be recognized more readily, and, hence, tend to be eliminated from the population.

If the effective population size is large enough, a considerable variety of chromosomes with diverse gene contents is to be found at all times in most breeding units. This does not refer merely to a sizable chain of alleles, but rather to linked groups of genes on a chromosome as a whole or on a segment of a chromosome. Natural populations appear to drift toward a balanced heterozygous state.

Most natural populations appear to be mixtures of individuals that are homozygous for some genes and heterozygous for other genes, and also heterozygous for gene arrangements. Gene arrangements have been found to vary in populations with some reference to geographical areas.

An experiment by Dobzhansky and Levene (1951) in relation to heterosis in wild populations of *Drosophila* produced some very interesting results, that appear to have considerable significance to livestock breeders. The investigators worked with strains of flies from three distinct geographical areas. Strains derived from the three areas are known as *ST*, *AR*, and *CH*, respectively. The heterozygotes produced from strains within the same geographical area, e.g., *ST*, were found to be superior as a rule in adaptive value to homozygotes. On the other hand, heterozygotes produced from crossing strains arising from different geographical areas, e.g., *ST* and *AR*, exhibited no superiority in the F_1 population over the parental types. In later generations, however, heterozygous types segregated which proved superior to the parental types.

The interpretation of an experiment such as that described above offers possibilities of application to livestock, but the possibilities are naturally subject to considerable error. The fact that the strains subjected to natural selection for adaptability in the same area exhibited a greater adaptability in the heterozygous state than in the homozygous state indicates that it is possible to develop strains or lines for the same characteristics (in this case, adaptability to the area), and yet obtain hybrid vigor when such strains or lines are crossed. The experiment certainly gives no support to the belief that the best method of

obtaining maximum hybrid vigor is to cross a line low in fertility but high in rate of gain with one high in fertility and low in rate of gain.

A further very interesting point, one that appears to have considerable practical significance to livestock breeders, is that the F_1 population obtained from crosses of flies from different geographic areas exhibited no heterosis in the F_1 population, but that later generations exhibited superiority. This, the investigators believe, may have resulted from an extensive "shuffling" of the genetic factors, which in later generations resulted in superiority. Put in more concrete and direct form, it means that the animal breeder may introduce foreign genes into a line of livestock which would exhibit no improvement in the first cross, yet a benefit might appear in subsequent generations after the genes had been efficiently reorganized. It also suggests that in countries such as Great Britain, which possesses a large number of breeds in a rather small area, the livestock industry might do well to develop a program of reducing the number of breeds through the process of recombination or synthesis of lines as discussed in Chapter XIX. Some Britishers believe that they suffer from a surplus of breeds. The elimination of a breed or breeds might eliminate useful genes, but by combining breeds and reshuffling the genes new opportunities for superior gene combinations are offered.

Speculations can be made in regard to the results of inbreeding and of methods of developing and maintaining inbred lines. They give some support to the view that a certain level of inbreeding may be very useful in developing the proper balance between homozygosity and heterozygosity and in the development of a balanced heterozygosity. This may account for the relatively high performance of some inbred lines of swine in contrast to the low performance of the more highly inbred lines of corn. If this is true, then the animal breeder may do well to raise the inbreeding level of his stock to the optimum level (he will have to find that level) but hold it near that level in order to preserve the heterozygosity of favorable gene combinations.

The above-mentioned experiments also indicate that an attempt to develop inbred lines from small populations is much less likely to be successful than from large populations. The experiments give support to the view that a flexible system of

breeding is more likely to "shuffle" the genes more thoroughly than a fixed system (one-sire or two-sire system) of breeding.

If, then, it is to be accepted that for practical purposes it is better to retain what may be called a somewhat balanced heterozygous state in inbred lines of farm animals, it is highly imperative that the lines be maintained on a rigid program of production testing. This will be necessary to guide culling the undesirable recombinations of genes that will continue to appear. It will also be necessary to maintain essentially closed herds in order to maintain both some purity and the balanced heterozygosis state.

What does all this have to do with purebred breeding? It is difficult to be positive on that score, because, as pointed out above, there are differences between wild populations left to "the survival of the fittest" and herds and breeds under man's guidance. The value to the breeder would appear to be that, by learning what happens to the genetic structure of a population left to seek its own level, the breeder should develop hypotheses as to better methods of working with nature to achieve his own purposes. In this case it indicates at least that the establishment of "closed populations" is a sound approach. The establishment of herdbooks was a sound beginning. It would appear that smaller, essentially closed groups within the existing breeds would be a further step in the direction indicated. What is the optimum size for such populations is not clear. It may be that the inbred lines being developed experimentally are the correct size. On the other hand, it may be that larger herds such as the great Hereford herd developed by Robert H. Hazlett at Eldorado, Kansas, are more nearly optimum. The author is inclined to believe that optimum size will vary with different genetic materials.

The studies indicate that optimum vigor will, however, be realized when two or more closed populations are crossed systematically.

Modern research in genetics indicates that the purebred industry of the future will undoubtedly be different from what it is today. It also indicates that the over-all program of pedigree breeding has been sound, but that it is time to move on.

The Purebred Breed of the Future. A new philosophy is rapidly taking root in livestock breeding. The period of con-

tinuous expansion seems to be at an end, and it appears that the next step will be an intensive program of improvement in efficiency. The development of inbred lines seems likely. These lines will need to be maintained intact by the most advanced breeders. Others will draw on these more highly purified lines for the production of line crosses, and the line crosses will probably be used by commercial producers for breed crosses.

Constructive animal breeding seems to be entering the professional era. Several producers of hybrid seed corn have interested themselves in this newer movement in both poultry and swine. The newer movement calls for more and more precision and system. The work is rapidly becoming highly professional. Cochrane (1945) has the following interesting comments to make on this point:

Breeding is not an occupation lightly to be undertaken, by those who have given no thought to what it involves. If the owner is not prepared to take on these responsibilities—to give the time and attention and study they require—he is better advised to obtain the services of someone else. But whoever he employs to run his herd, the direction of policy must be his own responsibility. Thus, it is his fault, even if he has nothing to do with the herd himself, if it is run solely for showing, or for obtaining maximum profit with the minimum trouble. Now, it is hard to find a man capable of undertaking constructive breeding, but it is ten times more difficult to find one capable of breeding efficient cattle. To concentrate on efficiency—if one is concerned with pedigree cattle—requires not a little courage and self-reliance, apart from a thorough knowledge of breeding in all its aspects. Such a man is unlikely to be found among those whom the nation has not seen fit adequately to educate; still less, among those who cannot be educated.

The changes that appear in the offing will call for more rather than fewer producers of good seed stock; such has been the result wherever improved technics have been used in plant breeding.

CHAPTER XVI

Grading

Grading is the mating of scrub or grade females to a purebred sire. Many advocates of livestock improvement have come to regard grading as the most, if not the only, acceptable method of improving commercial livestock.

Improvement Rapid. By the continued use of good purebred sires only a few generations are required to bring the herd to the point at which it has all the appearance, actions, and practical value of purebreds. Table XL shows the rapidity with which purebred sires will change the genetic constitution of a herd.

TABLE XL. GENETIC CHANGE BROUGHT ABOUT BY THE USE OF PUREBRED SIRES ON A SCRUB HERD

Generation	Offspring	
	Per Cent Replaced	Per Cent Scrub
1	50	50
2	75	25
3	87.5	12.5
4	93.75	6.25
5	96.87	3.12
6	98.44	1.56
7	99.22	0.78

Figure 83 illustrates the principle of grading by a different method; the replacement of breeding is put on the chromosome basis. Cattle have 60 chromosomes or 30 pairs. If a cross between the Hereford and Shorthorn breeds followed by continuous backcrossing to the Hereford breed is assumed, the average chromosome number of each breed in each generation is shown in Fig. 83. The exact number of Hereford and Shorthorn chromosomes in any one individual is, however, subject to considerable variation.

Table XL and Fig. 83 should make clear how topcrossing with superior sires will in a few generations bring about a substitution of desirable genes for undesirable ones. The same principle applies whether the practice consists in using purebred sires on a scrub foundation or sires backed with outstanding performance on a foundation of stock in which the performance is questionable.

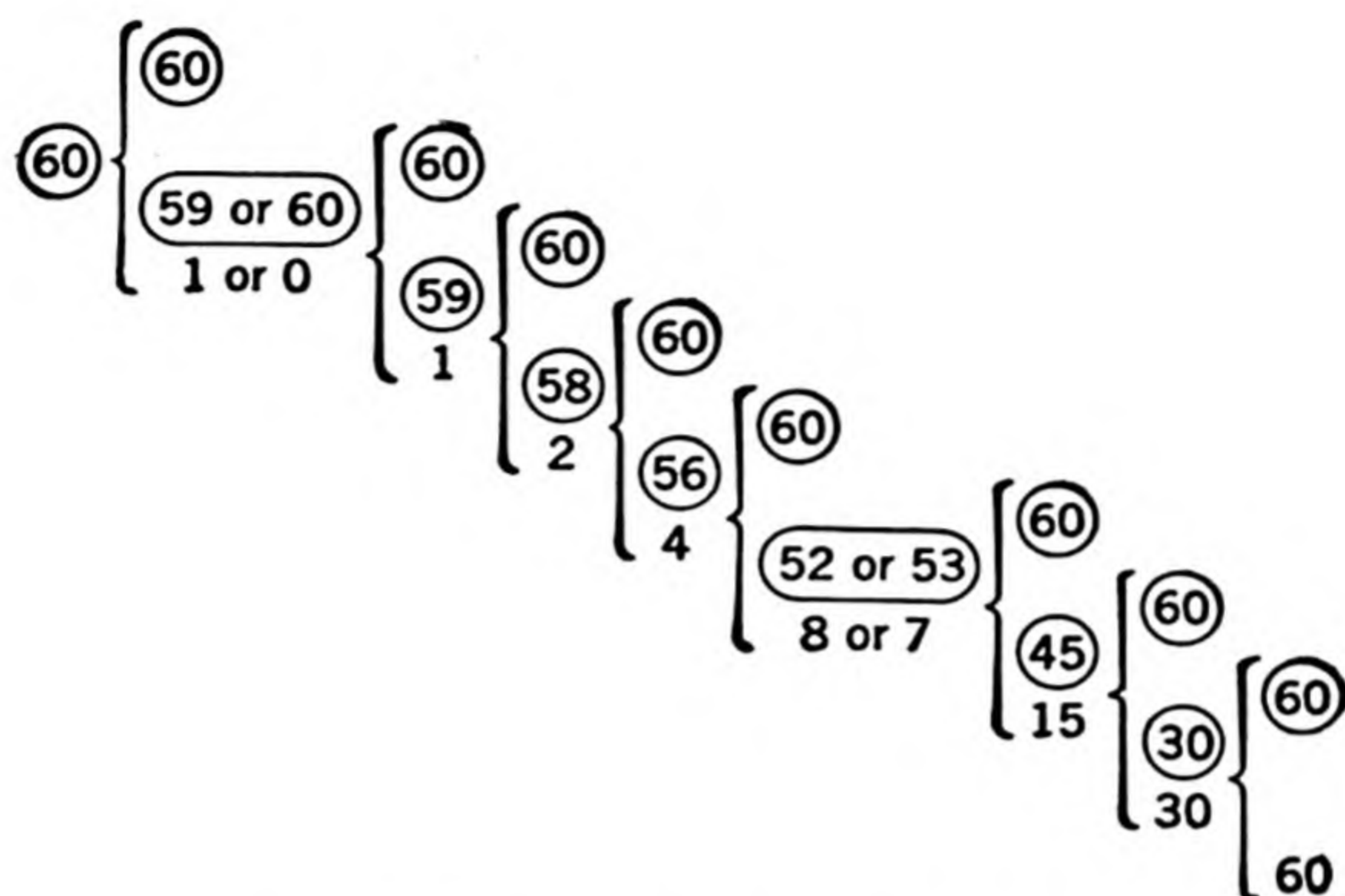


FIG. 83. The approximate Shorthorn and Hereford chromosome numbers in each generation as the result of first crossing the two breeds and then continuing to backcross to the Hereford. The numbers in the circles indicate Hereford chromosomes, and the uncircled numbers, Shorthorn chromosomes. (In studying the above it should be kept in mind that after the first generation the numbers are approximate rather than definite.)

The above-mentioned table and illustration make clear also the relative importance of the individual's various ancestors; the individual ancestor beyond the first three generations bears a rather slender relationship to the individual in question.

The principles of grading apply to any class of stock, but the most significant experiments were conducted with dairy and beef cattle; hence only those will be reviewed.

Grading Dairy Cattle. An experiment to test the possible improvement in milk production by the use of good purebred dairy bulls on scrub females was started at the Iowa State College in 1907 (Kildee and McCandlish, 1916; McCandlish, Gillette, and Kildee, 1919; Weaver, Matthews, and Kildee, 1928). A summary of the improvement in production accomplished in two generations by the use of good purebred dairy sires is given in Table XLI.

TABLE XLI. IMPROVEMENT IN PRODUCTION BY GRADING WITH PUREBRED DAIRY BULLS AT THE IOWA STATION

(After McCandlish, Gillette, and Kildee, *Iowa Bulletin* 188)

Group	Number of Cows	Number of Lactations	Average Production	
			Milk, Pounds	Fat, Pounds
Scrub dams	5	23	3,660.2	171.57
First grades	5	21	5,998.7	261.25
Second grades	5	6	8,401.9	358.17
Increase in production 1st generation			2,338.5	89.68
Increase in production 2nd generation			4,741.7	186.60
Increase in production 1st generation			64%	52%
Increase in production 2nd generation			130%	109%

In two generations, the improvement in production, by the use of good purebred dairy sires, was well over 100 per cent; one of the granddaughters was doing more work than two of the old scrub granddams. There was a similar change in type; the second-generation grades possessed much of the appearance of the breed to which they were graded. The maximum and most economical production, however, was reached in the third generation; the fourth generation of grades fell short of the third generation in both respects.

In a somewhat similar experiment, conducted by the South Dakota Agricultural College, grade Shorthorn and Hereford cows served as a foundation. Continuous grading with purebred Guernsey, Jersey, and Holstein-Friesian bulls, respectively, was practiced; the results are summarized in Table XLII.

Grading Beef Cattle. W. R. Nelson of Kansas City, Missouri, was of the opinion that the farmers of the Missouri Valley were not raising sufficiently typed beef cattle. He set about to demonstrate what could be accomplished through the use of good purebred Shorthorn bulls on common female stock. The founda-

TABLE XLII. IMPROVEMENT IN PRODUCTION BY GRADING WITH
PUREBRED DAIRY BULLS AT THE SOUTH DAKOTA STATION

(After Olson and Bigger, *South Dakota Bulletin* 198)

Group	Number of Cows	Number of Lactations	Average Production	
			Milk, Pounds	Fat, Pounds
Dams	7	50	4,155.2	170.56
First grade	9	28	6,707.4	260.06
Second grade	7	14	6,267.6	267.64
Increase in production 1st grade			2,552.2	89.50
Increase in production 2nd grade			2,112.4	97.08
Increase in production 1st grade			61%	52%
Increase in production 2nd grade			51%	57%

tion cows consisted of 200 common red cows typical of cattle then being raised in the Missouri Valley. Some of the cows were in calf. Thus one crop of calves unimproved in breeding was reared and marketed under the same conditions as the later grades. Since no production records were kept, it is impossible to make comparisons between the various generations except in conformation and market price. Since the different groups were marketed necessarily at different times, each group is compared to the top price brought by other cattle reaching the same market during that same week. A summary of the results is presented in Table XLIII.

This experiment demonstrated that the use of good purebred beef bulls resulted in the production of beef steers that were more acceptable on the market and sold at materially higher prices than the steers of unimproved breeding.

A significant experiment in grading beef cattle was conducted in Arkansas. The experiment included three crops of purebred Aberdeen-Angus calves, native Arkansas calves, first-cross calves, and second-cross calves. The results are summarized in Table

TABLE XLIII. SUMMARY OF GRADING WITH SHORTHORN BULLS
AT THE SNI-A-BAR FARMS UP TO 1921

Breeding	Num- ber	Market Price		Over or under Top	Price Propor- tionate to Top
		Top of the Week	Sni-A-Bar Cattle		
Unimproved	30	9.62	7.88	−1.74	.82
1st cross	82	11.57	11.30	−0.27	.98
1st and 2nd crosses	184	14.84	16.05	+1.21	1.08

TABLE XLIV. SUMMARIZED RESULTS OF THREE YEARS' STUDY OF
GRADING NATIVE ARKANSAS CATTLE WITH PUREBRED
ABERDEEN-ANGUS SIRES

(Abbreviated from Semple and Dvorachek)

	Pure- bred Calves	Second- Cross Calves	First- Cross Calves	Native Calves
Cost of weaning per head	\$41.20	\$37.63	\$32.95	\$35.12
Feed cost to fatten per head	\$30.36	\$30.05	\$29.49	\$26.62
Total feed cost per head	\$71.56	\$67.68	\$62.44	\$60.74
Sale weight per head	672.86	676.52	664.50	630.48
Net sale value per head	\$74.62	\$74.08	\$70.17	\$61.98
Difference between sale value and total feed cost per head	\$3.06	\$6.40	\$7.73	\$1.24
Net sale price per 100 pounds	\$11.09	\$10.95	\$10.56	\$9.83
Shrinkage in transit, percentage	5.00	4.84	4.78	6.29
Cold-dressed percentages	58.15	58.85	57.96	57.03

XLIV. In a summary of the study, Semple and Dvorachek (1930) state:

Three crops of weanling calves were produced considerably more cheaply per head and per 100 pounds live weight from native Arkansas cows than from purebred Aberdeen-Angus cows, because the grade and native cows were smaller and required less feed in winter than the purebred cows. . . .

When running on pasture with their dams, without supplementary feed, grade and native calves made greater gains to weaning time than

purebred calves. These average daily gains for the three years were 1.59, 1.68, 1.71 and 1.69 pounds, respectively, for purebreds, second crosses, first crosses, and native calves.

While there was practically no difference in the feed required per 100 pounds of gain for purebreds, grades, and natives fattened after they were weaned, the purebred calves ate slightly more and made somewhat greater gains than the grade or native calves. The average cost of producing 100 pounds of gain was \$10.76, \$11.14, \$10.82, and \$10.97, respectively, for purebreds, second crosses, first crosses, and natives for the three years.

The combined costs up to weaning time and of fattening were less for native calves, but the sale price of purebreds and grades was enough higher so that the sale value of purebreds and grades more than made up the difference in lower total feed costs of the natives. When the average total feed cost was taken from the average sale value for each lot, the return above feed costs was \$3.06, \$6.40, \$7.73, and \$1.24 a head for the purebred, second-cross, first-cross, and native calves, respectively. These returns indicate the value of service of a purebred sire on native cows. The first-cross calves made a return per head of more than six times as much as the native calves, or a difference of \$6.49 a head.

The Arkansas experiment shows very clearly the advantage to the producer of using good beef bulls rather than native bulls on the native cows. It also shows that the straight purebreds were not so profitable for beef production under Arkansas conditions as the first- and second-cross calves. The native stock apparently possesses an adaptability that has economic value.

Limitations of Grading. Grading does not have all the advantages frequently attributed to it. In some of the experiments set up to demonstrate the economic advantages of grading the sires used were higher priced than would have been practical for use in commercial livestock production. It is frequently overlooked that maximum improvement is made during the first and second top crosses, and that these crosses, in some instances at least, benefit not only from the use of superior sires but also from a certain amount of hybrid vigor.

Although improvement is rapid from generation to generation, it is slow in years especially for cattle and horses. In many instances farmers should follow the English practice of purchasing breeding females from other farmers or ranchers who are more favorably situated to produce surplus female stock economically.

In England the farmer after purchasing his female stock mates them to an outstanding sire, generally of another breed, and markets all the offspring. The females and the sire are retained as long as they are useful. The farmer is thereby allowed a much greater turnover each year, and the size of his herd or flock is reduced because he does not need to save young animals for replacements. Since by this method the good sire is maintained as long as he remains fertile, the farmer can afford to pay more for an outstanding male.

CHAPTER XVII

Fertility

The function of breeding animals is the regular perpetuation of their kind; therefore, the degree of fertility within a herd, flock, or stud has a direct bearing on the profits from that herd, flock, or stud. No breeder, of either commercial or breeding stock, can afford to keep unproductive animals. In dairy cattle there is the added loss of reduced milk production.

Not only are the more fertile females more profitable, since a given number of females will reproduce more offspring that can be marketed, but also they offer the constructive breeder, especially the new breeder, a chance to cull his breeding stock more closely. If three breeders start in the hog business with 1 sow each, the average litters of each sow and her descendants being 4, 6, and 8 pigs, respectively—one-half of which are, in each case, males—and if the old sows are retained for five years, the number of females available for breeding purposes each year will be as in Table XLV.

TABLE XLV. THE EFFECT OF FERTILITY UPON INCREASE OF BREEDING STOCK

	Sow 1	Sow 2	Sow 3
Offspring per litter	4	6	8
Breeding females available 2nd year	3	4	5
Breeding females available 3rd year	9	16	25
Breeding females available 4th year	27	64	125
Breeding females available 5th year	81	256	625
Breeding females available 6th year	243	1,024	3,125

Probably none of the three breeders would want all the females available even before the sixth year was reached; but the owner of sow 2 would each year have been able to make a larger turnover in proportion to his capital investment and in proportion to

his feed and housing costs than the owner of sow 1, and the owner of sow 3 would have exceeded both.

A high degree of fertility is important in constructive livestock breeding. Let it be assumed, as above, that the average size of litters in three herds is 4, 6, and 8 pigs, respectively, and let it be assumed that each breeder maintains a 20-sow herd. Considering old stock as well as gilts, the first breeder retains 1 female out of 3, and the third retains 1 of 5, or in gross terms they have the choice of 20 females out of 60, 80, and 100, respectively. For the breeder who is selecting closely and on the basis of a number of factors, the higher fertility is of special advantage. It is prerequisite to effective selection for rate of gain, economy of gain, body form, and the like. Comstock and Winters (1944) calculated the selection differentials actually attained in the Minnesota inbreeding project (Table XLVI). It

TABLE XLVI. SELECTION DIFFERENTIALS ATTAINED IN POLAND CHINA LINES AT MINNESOTA

(From Comstock and Winters, *Jour. An. Sci.*)

Sex	Litter Size at Birth, Pigs per Litter	Average Daily Gain, Pounds	Body Score	Feed per 100 Pounds Gain, Pounds
Gilts	1.12	0.107	2.7	-1.5
Boars	1.12	0.155	2.8	-0.7

is quite apparent that if litter size had been larger the selection differential would have been larger for all factors considered.

In the species with lower fertility, such as sheep and cattle, the problem of fertility is a much greater limiting factor than in swine. In these species the degree of fertility is affected to a large extent by longevity or at least by the duration of fertility in the females.

Degree of fertility has an important bearing on the development of a system of breeding best adapted to specific purposes. A difference in fertility may make a degree of fertility that is satisfactory for one species unsatisfactory for another. The difference in the degree of fertility between corn and hogs is sufficient to make methods that are satisfactory in corn unsuited to swine. The constructive animal breeder, therefore, has to try to

get more out of each individual because of his more limited numbers.

Fertility is one of the important problems confronting the livestock breeder. It, like most of the problems in livestock production, is affected by many factors; therefore, the problem of fertility is to be solved by an understanding of all the factors.

Heredity and Fertility. Like all characters fertility is limited by heredity. As stated in Chapter VII, an inherent capacity for a certain degree of fertility is no assurance that the individual or line will perform to that degree.

The differences in fertility between species is clearly marked. Breed differences also exist but are less marked than species differences. Coffey (1918) gives the average percentage of lamb crop for several breeds of sheep as shown in Table XLVII.

TABLE XLVII. BREED AS A FACTOR IN FERTILITY

Breed	Per Cent Lamb Crop
Southdown	125-150
Shropshire	150-175
Hampshire	119+
Suffolk	133

A number of statistical investigations on the inheritance of fertility in all species of farm animals clearly demonstrate differences between certain breeds, families within breeds, and progeny of different sires. In addition, certain genital anomalies, which may reduce the degree of fertility or result in complete sterility, have been shown to be heritable.

Several genetic studies of laboratory animals have demonstrated that fertility is governed by hereditary factors, that is, that hereditary factors limit the individual's reproductive capacity. Morgan (1919) gives ample evidence that gametic and zygotic lethals are often responsible for reduced fertility and even for sterility.

Many more estimates of the heritability of fertility have been made with swine than with other classes, mainly because swine are more prolific and the variance in the degree of fertility is therefore more accurately treated statistically. From a study of the Minnesota data, Stewart (1945) and Cummings *et al.* (1947) reported heritability estimates of fertility in swine of 17 per cent

and 19 per cent, respectively. Estimates of heritability of fertility in sheep as reported by Desai (1950) from a rather extensive analysis of Minnesota data were very low. His estimates were 0.03 and 0.07, and the repeatability of twinning was 0.05. In the latter case it would seem that the degree of fertility is quite well fixed early in the development of breeds of sheep and that there is little opportunity to change the inheritance of fertility through selection alone within the limits of a particular population. The heritabilities of fertility in swine also are low, particularly in contrast to the estimated heritability of many other characteristics. This contrast may mean that fertility is especially subject to environmental influences. It may also mean that the character is less influenced by additive gene effects, or it may mean that the genes affecting fertility are rather well fixed. In any event, present evidence indicates that improvement of fertility by individual selection will not be rapid.

A low degree of fertility may result from a deficiency in any one or several of the complex physiological processes involved, and these functions may be influenced by heredity. Hammond (1934) reported two strains of rabbits with very low fertility. In one strain, the ovulatory rate was low but they showed a high prenatal survival. In the other strain, the ovulatory rate was quite high but the prenatal death rate was also very high. When these two strains were crossed the resulting fertility was good, yet the crosses did not exceed the high strain in ovulatory rate or in the rate of prenatal survival. This demonstrates the possibility at hand for livestock breeders to improve fertility in stock of low fertility, if, after an outcross for higher fertility, the offspring are inbred and rigorous selection is used.

Generally a higher degree of fertility results from crossbreeding. The results with swine (Winters *et al.*, 1935) showed more pigs per litter in the first crosses from purebred dams and even a higher litter size in the three-breed crosses. There was undoubtedly more vigor in the F_1 pigs themselves, resulting in a lower mortality rate during prenatal life. The same thing also occurred in the three-breed crosses, and at the same time the reproductive processes of the crossbred dam were more efficient. The same general increase in fertility from crossbreeding is observed in other classes of animals. The opposite is likely to occur with inbreeding if little attention is paid to selection for

fertility. Thus it is very important to select rigidly for fertility in the development of an inbred line in order to maintain it at an economical level.

Type and Fertility. There is an assumption among stockmen that animals of certain types are more fertile than those of other types. The belief is that compactness of form is associated with a lower level of fertility; it is then reasoned that animals of this type do not have sufficient room for the reproductive organs. Phillips and Zeller (1942) and Hetzer and Brier (1940) present evidence that large type in Poland China swine is associated with a higher degree of fertility. They report that the large-type females produced litters which averaged 7.4 pigs and the small-type 5.8 pigs per litter. They found that the large type reached sexual maturity at an earlier age. Care, however, needs to be taken in making broad interpretations from data such as these. They pertain to the Poland China breed only. In contrast, the Hampshire is not a long-bodied hog, yet the fertility is generally recognized as rather high. Phillips and Hsu (1944) in a report on Chinese swine show illustrations of short-bodied pigs that have slow growth rates and high fertility. They also report exceptionally early sexual maturity in the Chinese swine.

If type is associated with the degree of fertility, it appears more likely that a certain type and a certain degree of fertility are affected by the same level of hormone production. This similarity, however, eventually traces to a genetic foundation; the different levels of hormone production are, therefore, the means of carrying out the individual's genetic constitution, and the different types and levels of fertility are the results.

Age and Fertility. Every breeding female rises from infertility to increased fertility, usually reaching the peak early in her full maturity; she then gradually declines until she is again infertile. The situation is essentially the same in the male.

A ewe reported by Pearl (1913) conforms to the above very closely: she had single lambs the first two years, twins the third year, triplets for the next six years, twins for the following six, and singles for the remaining two years of her fertility.

Studies made at Wisconsin and presented briefly in Table XLVIII show that the age of ewes is a factor that influences the

TABLE XLVIII. EFFECT OF EWE'S AGE UPON PER CENT OF LAMB CROP

Age of ewes	2	3	4	5	6	7
Average per cent lamb crop	158	174	178	177	178	150

percentage of lamb crop. It is quite generally believed that the number of ova ripened during oestrus is the factor that governs the percentage of lamb crop, provided the ram used is fertile; but in these studies it was found that this was not necessarily true. Over a period of six years, yearling rams got, on the average, a 150 per cent lamb crop; whereas two- and three-year-old rams, each used three years, got an average crop, for the six years, of 180 per cent.

Studies, made by Rommel (1907), of the records of Poland China sows during 1902 show that, in general, a sow does not reach the height of her prolificacy until she is five years old. A summary of the work is presented in Table XLIX. In this study,

TABLE XLIX. EFFECT OF SOW'S AGE UPON SIZE OF LITTERS IN POLAND CHINA SOWS

Age	Number of Sows Studied	Average Size Litter
1	1,520	6.5
2	2,047	7.5
3	1,157	7.9
4	606	8.3
5	325	8.7

one reason for the older sows' averaging more pigs per litter was no doubt the fact that only those sows proving more prolific than the average were retained.

Stewart (1945) studied the Minnesota data and found that gilts grow in fertility; litter size among gilts increased with the age of the dam but the rate of increase declined and no increase was found after 15 months (Fig. 84).

Age of First Breeding and Fertility. The age at the time of first breeding undoubtedly has an influence upon the female's later fertility, but the degree has not been determined by experimental work. It is believed by stockmen that, if the first breeding is delayed too long, conception becomes more difficult; on the other hand, if the female is bred too early in life she

seldom gains full maturity or her full inherent vigor; thus her life is shortened, and her breeding powers are curtailed.

The most desirable age of first breeding is subject to variations dependent to a certain extent upon species, breed, and the feed and care received. In general, individuals of the early-maturing breeds can be bred at an earlier age than those maturing later, and individuals that have been well fed and are well grown can be bred earlier in life than those not so favorably handled.

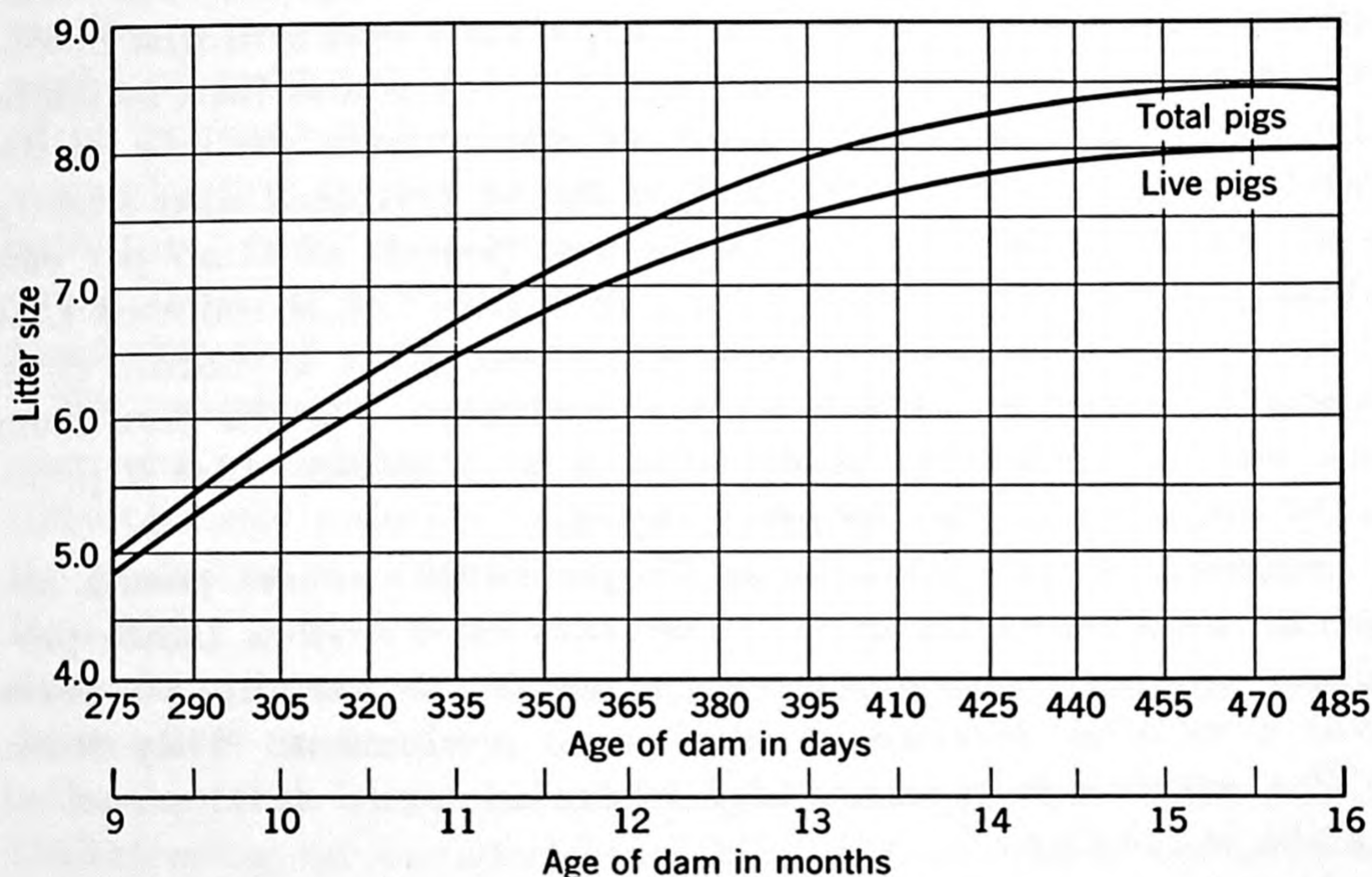


FIG. 84. The effect of age of dam on the number of pigs born. (After Stewart.)

Studies on the effect of breeding range heifers to drop calves as two-year-olds were made by Lantow (1922) through correspondence with sixty-six ranchers. From the replies to the question: "Do heifers which produce calves as two-year-olds produce calves at three?" the conclusion was drawn that, by breeding to calve at two, a year was lost in over one-half the cases, and that, furthermore, most of the heifers were stunted.

To the questions: "Do you get a higher percentage of calves from heifers bred to calve at three years than at two? If so, how much greater?" thirty-eight answered yes, six answered no to the first question, and the average to the second question was 29 per cent increase.

To the question: "At what age are your heifers bred to calve?" the average answer given was two years, four and one-half months; the only valid excuse given for breeding to calve at two years was that the calves were needed at once for ready cash.

Early breeding no doubt decreases the female's breeding powers through retarded development, possibly the worst effect of early breeding; therefore, the question of time of first breeding is closely related to the individual's state of nutrition.

The North Dakota Experiment Station (Longwill, 1942) conducted a long-time study of the comparative effects of first breeding ewes as lambs and as yearlings. The ewes first bred as lambs produced more lambs and more pounds of lamb per ewe on the lifetime basis. The ewes bred as lambs produced also slightly but not significantly more lambs and pounds of lamb per ewe during the second to fifth years, inclusive. It is reported that the two groups of ewes did not differ noticeably as mature ewes. Longwill concluded, however, that the crop of lambs born from the ewes when lambed as yearlings was so inferior that it probably did not pay for the extra expense.

Spencer, Schott, Phillips, and Aune (1942) report results opposite to those of Longwill. The ewes bred first as lambs produced slightly less wool, about 0.3 pound less per clip, but there was a material increase in total lamb production. They state, "This practice is recommended where adequate development of lambs is obtained."

Nutrition and Fertility. As noted above, feed has a very important effect upon the individual's degree of fertility. In the studies of Lantow referred to above, the question was asked: "Do heifers bred to calve at two years old, when winter-fed both years, drop calves at three? What is the percentage of the calf crop from these three-year-olds?" The consensus was that the majority of the three-year-olds would drop calves, the average of the replies being 78.8 per cent, which is about a normal average under range conditions. These questions were followed by: "Do heifers bred to calve at two years old, when not winter-fed either year, drop calves at three years old? What is the percentage of calf crop from these three-year-olds?" The replies indicated that such three-year-olds do not usually drop calves, the average being only 18 per cent. Comparing the answers to these questions with the preceding ones indicates that a 60 per

cent greater calf crop may be expected from three-year-olds that are bred to calve first as two-year-olds, provided they are winter-fed.

Shepherds have long been aware that "flushing"—getting the ewes in a rising condition previous to breeding—results in a larger lamb crop. The results of experiments run for six years by the United States Department of Agriculture were that "flushed" Southdown ewes produced 198 more lambs per 1,000 ewes than non-flushed ones. Flushing is accomplished by turning to a fresh pasture or by feeding one-fourth to one-half a pound of grain per day. The same practice has been put into effect by many swine breeders with equally good results.

Overfeeding is just as detrimental as underfeeding, and it is regrettable that each year a considerable number of our best young females, especially beef heifers and ewes, are so highly fitted that they never become regular producers.

The practice of carrying breeding animals in show condition over long periods appears to have disastrous effects on the fertility of many animals. The deep deposits of fat in and around the genital organs appear to be detrimental to their function. It is likely that the general effect of carrying an excess of fat slows functioning of the endocrine system and that this has a direct effect on fertility.

On the other hand, underfeeding may be equally detrimental. Underfeeding on an adequate ration will not have an adverse effect nearly so quickly as when the ration is deficient in some particular constituent. Rations deficient in vitamin A lead to sterility but only after the deficiency has become so pronounced that considerable damage has been done in other respects. Therefore, reduced fertility is secondary to the main effects of vitamin A deficiency. The B vitamins and vitamin C are important to normal fertility. Deficiencies due to lack of the former are unlikely to occur in ruminants since they are capable of synthesizing these nutrients; however, caution should be taken that the B vitamins are adequately supplied in the diets of other classes of livestock. Generally, sufficient vitamin C will be present in normally balanced rations which include well-cured roughages of good quality. Much has been written about vitamin E and its effect on fertility. Recent work, however, indicates that

vitamin E is not necessary for reproduction, in some species at least.

Rations deficient in any of the minerals, to the point that the animal's normal growth and development have been impaired, will lead to reproductive disturbances. The same is true for all other nutrients. In general, a balanced ration fed in sufficient quantity for normal growth and development will be sufficient to carry out normal reproductive processes. Naturally pregnancy (particularly the latter third) and lactation demand additional amounts of all nutrients for the female, and allowances must be made at these times in order for her to complete her task of producing young.

Environment and Fertility. It is the experience of stockmen that females receiving regular exercise and unstinted fresh air are more likely to raise a full crop of young the following year than those confined to close quarters. The same applies to males. The far too common practice of penning the ram and boar in small pens, and of tying the bull or stallion in the most out-of-the-way corner of the barn, with no exercise and little care between breeding seasons, is to be deplored; it is destined to result in a decreased get by those males. Both mares and stallions will breed more regularly if given a reasonable amount of work throughout the year.

The immediate effect of increased exercise is often a drop in the degree of fertility rather than a rise. In the practice of developing show herds young animals frequently go through the entire growing period in a very high condition and with very little exercise. After the animal has won its laurels it is put into the breeding herd. By this time the degree of fertility is frequently too low. Then an attempt is made to restore the animal's fertility through increased exercise and decreased feed. The animal is soft and forced exercise results in overheating which is disastrous to fertility. In time some of the animals can be returned to a fairly fertile condition, but too many are ruined permanently. The proper time for the exercise is during the growing period with perhaps more moderate amounts thereafter.

Sheep and goats are seasonal breeders, with their breeding season occurring mainly in the fall of the year. Some breeds do not follow this order entirely and may breed twice a year. A gradual decrease in the length of daylight over a period of sev-

eral weeks seems to be the primary stimulus which in turn controls the endocrine function of the pituitary gland. Many attempts have been made to alter their breeding season by inducing oestrus with injections of the gonadotropic and estrogenic hormones during the spring of the year in order to get two crops of offspring per year. Considerable variation has occurred in the results thus far, to the extent that the repeatability in success from such treatments has been very poor. Undoubtedly, other environmental stimuli and their interaction with changes in the extent of daylight are playing an important rôle.

Seasonal variations in the degree of fertility in the bull and ram have been noted. Both show a marked decline in semen production during the summer months and a further decline under extremely hot climatic conditions. Comstock *et al.* (1943) reported that a high condition and long fleeces on rams during summer months had unfavorable effects on semen production.

Reproductive Failures. The physiology of reproduction is a very intricate and complex process interrelated with nearly all other functions of the body. In some instances, a specific condition or a particular disease can be identified as the cause of reproductive failure. In other cases, no apparent reason for sterility or lowered fertility can be ascertained. However, the causes of reproductive failure can most frequently be found among the following: (1) anatomical defects; (2) mechanical injury of the genitalia; (3) infectious diseases; (4) prenatal death of the young; (5) physiological disturbances, particularly improper hormone balances; (6) gametic incompatibility; (7) low vitality of gametes; (8) failure to mate at optimum time during the oestral period; (9) psychic incompatibility; (10) impaired nutrition; (11) miscellaneous environmental disturbances; and (12) genetic causes which may be directly or indirectly related to the above factors.

Tanabe and Casida (1949) studied the nature of reproductive failures in cows of low fertility on a carefully selected group of 104 such cows. The cows showed no detectable genital abnormalities but had been "repeat breeders" for at least four times. All the cows had previously calved at least once. They were inseminated artificially and slaughtered on either the third or thirty-fourth day following breeding. At 3 days 66.1 per cent of the cows examined had fertilized ova, but at 34 days only 23.1

per cent had normal embryos. Visible genital abnormalities not detected by clinical examination were found in 10.6 per cent of the animals, and 8 per cent were physical barriers to fertilization. These cows could be divided into three groups: (1) failure of fertilization, 39.7 per cent; (2) embryonic abnormalities and mortality before 34 days, 39.2 per cent; and (3) normal pregnancies at 34 days, 21.1 per cent.

Warnick *et al.* (1949), studying the nature of reproductive failures in sows and gilts, found that repeat breeding was due to failure of fertilization in 53.4 per cent of the gilts and 32.6 per cent of the sows observed. Accountable failure of fertilization due to bilateral tubal abnormalities, bilateral missing segments, or bilateral cystic ovaries comprised 50 per cent of the gilts and 15.8 per cent of the sows. Embryonic death was responsible for repeat breeding in 23.9 per cent of the gilts and 67.4 per cent of the sows. Thus, the major cause for repeat breeding in gilts appeared to be failure of fertilization due to genital abnormalities, whereas in sows it was primarily caused by embryonic death.

Studies at Minnesota and other experiment stations indicate that prenatal death and resorption in swine are one of the most important causes, if not the most important cause, affecting the degree of fertility. It appears that, if it is possible for conception to take place, the fertilization rate is very close to 100 per cent. The resulting litter size is primarily due to the rate of embryonic mortality because there are nearly always many more eggs deposited, as determined by corpora lutea, than living young at term or at varying stages of pregnancy. The average rate of embryonic mortality during the first 25 to 30 days of pregnancy is between 25 to 30 per cent with an additional increase of 10 per cent from that time until the end of the gestation period. It has also been observed that the pig can die and be resorbed at any time during its prenatal life.

Hammond (1950) points out that a strong possibility for reproductive failures in cattle (and the same could be true of other classes) is too rapid passage of the ova down the Fallopian tubes. The result of this is that either the ova do not get fertilized, or, if fertilized, they pass to the uterus before it is in a properly receptive state and degenerate there. Ova can be "tube-locked" by excessive estrogen stimulation and speeded up down the tract by excessive progestin stimulation. Therefore, the

proper estrogen-progestin balance appears to be critical for this particular function.

Testing for Fertility. The final test for fertility is, of course, whether young are produced. The difficulty with that test is that it is too slow and expensive. Fortunately, through modern technics a rather satisfactory appraisal can be made of the male's relative fertility by examination of the semen in the laboratory. Some of the most valuable tests for semen quality are as follows:

1. Motility of sperm is still the best single appraisal of their vitality if it is carried out on a quantitative basis and with good judgment. Ordinarily this should be done by diluting a portion of the semen sample with a suitable clear semen diluter or with 0.9 per cent NaCl solution, placing a drop of this in a hanging drop slide, and examining it microscopically between $100\times$ and $500\times$ magnification. The dilution should be high enough so that the sperm cells are separated completely and their movement observed individually. Percentages of motile sperm can then be determined, and the various types of movement can be enumerated. The more viable samples will show a higher content of sperm that move rapidly in a straight line with little lost motion in the tail movements.

The phase microscope has made it possible to study motility and morphology of spermatozoa more accurately than has been possible with the regular microscope. High motility ratings of semen from bulls sampled in the above manner have a close association with the bull's fertility record in the field. It must be conceded that the movement of the sperm is not its sole means of ascending the female tract and fertilizing the ovum, yet it is an indication of general vitality of the cell, which includes other characteristics necessary to complete the processes of fertilization. Not all sperm that are motile are capable of fertilization, and, in rare instances, some samples of ejaculated semen showing no apparent motility outside the genital tract of the female are capable of fertilization.

An electrical method for measuring rate of motility of semen by means of an impedance bridge has been developed by the workers at Cambridge University (Rothschild, 1949). This method is more objective than the use of a microscope, since it eliminates the human error always encountered in microscopic examinations. However, it is limited to bull or ram semen since

the degree of swirl action as found in highly concentrated semen is what is actually being determined. The procedure involves placing a pair of platinum electrodes about one millimeter apart in a sample of freshly ejaculated semen. An alternating current of 50 millivolts and 5 kilocycles is then passed through the semen, and the impedance bridge is brought into balance with it. As the sperm cells move about in a swirling manner between the electrodes, the electrical field is disturbed and the impedance changed. These changes in impedance are indicated on an oscilloscope. The rate of movement of the sperm is proportional to the rate of impedance changes, and the latter is then used as an index of sperm viability in the particular sample tested.

During 1950 to 1953 research has been in progress at the University of Minnesota in cooperation with one of the dairy cattle artificial breeding centers in Minnesota, where semen samples from bulls used in artificial insemination have been collected and tested by a number of procedures (Cummings and Winters, 1953). Two of the main objectives of the study have been to determine the relationship between the results of these laboratory tests and the breeding efficiency of the bulls in the field and to develop a reliable semen-testing procedure that will accurately predict the breeding efficiency of the bulls. The Rothschild impedance bridge has been used extensively as one of these tests. The results are very promising and might very well prove to be the best single semen test for the evaluation of the fertility in bulls. The results of a four-month testing period given in Table L show the relationship between the rate of impedance changes of the semen and the breeding efficiency of the bulls tested.

TABLE L. THE RELATIONSHIP BETWEEN THE RATE OF IMPEDANCE CHANGES OF BULL SEMEN AND THE BREEDING EFFICIENCY OF BULLS TESTED

Rate of Impedance Changes per Min.	Average Breeding Efficiency of Bulls Tested, Per Cent Non>Returns in 30-60 Days	No. of First Services
126 and over	71	122
101-125	71	3,870
76-100	70	4,398
51-75	67	3,906
26-50	61	1,854
0-25	58	501

During the same investigations a high association was found between rate of impedance changes and the results of an additional laboratory test run on the same samples (Table LI). At

TABLE LI. RELATIONSHIP BETWEEN RATE OF IMPEDANCE CHANGES AND OTHER SEMEN CHARACTERISTICS

Rate of Impedance Changes per Min.	Number of Samples	Average Sperm Concentration, Millions per Cubic Millimeter	Average Motility (Microscopic)		Average Respiration Rate, Cubic Millimeters O ₂ per 0.125 Cubic Centimeter Semen in 1 Hour	Live Sperm, Per Cent	Abnormal Sperm, Per Cent
			Motile Sperm, Per Cent	Index *			
126 and over	10	2.45	81	67	44.07	86	10
101-125	45	2.14	71	58	30.67	76	10
76-100	58	1.89	69	45	27.95	75	11
51-75	66	1.64	62	39	19.58	67	12
26-50	87	1.42	50	26	17.08	62	17
1-25	63	1.01	48	26	14.81	61	14
0	11	0.55	19	13	6.50	32	7

* The motility index was determined by multiplying the percentage motile sperm by a factor indicating the types of motility found in the sample.

the same time this test gave a good indication of how well the semen would hold up under storage since the microscopic motility ratings, respiration rates, and percentage of live sperm were determined 24 hours after the semen was collected and the rate of impedance changes was determined immediately after collection.

2. Sperm concentration of semen can be determined by counting the number of cells in a known volume of fluid after the semen is diluted at a high but known rate. The regular hemacytometer counting chamber is used for this purpose but it is slow and tedious. The use of photoelectric calorimeters and spectrophotometers to measure the amount of light transmitted through a fine suspension of sperm are quite accurate and fast. The use of barium sulphate suspensions set up as standards to compare with semen diluted at a constant rate is also rapid and satisfactory (Comstock *et al.*, 1943). Average sperm concentrations for semen from various classes of farm animals are given in the following chapter.

Generally, denser samples of semen are more viable, but caution must be exercised in this evaluation since it is true only if they are equal in other respects. Males with good fertility records generally produce semen of high sperm concentration.

3. Measurement of special metabolic rates of sperm cells is quite useful in evaluating the relative fertility of different males. Those employed so far are: (1) respiration, the reactions which result in oxygen uptake; (2) glycolysis, rate of carbohydrate metabolism; (3) fructolysis, the rate of fructose utilization; and (4) the rate of methylene-blue reduction.

Respiration is most accurately measured by a Warburg apparatus, but a simpler type of apparatus which is portable has been designed by the workers at the University of Minnesota, and it is satisfactory for comparisons where extreme accuracy is not required (Comstock *et al.*, 1943). The higher respiratory rates of semen indicate greater viability both in respect to livability of the semen under storage conditions and in respect to its fertilizing capacity. The following table includes some results by Walton and Edwards (1938), showing the relationship between service records of bulls and the respiration rates per million sperm of semen samples from the same bulls when an exhaustion method of collecting was used:

No. of Bulls	Services per Conception	Av. Initial Resp. Rate	Av. Resp. Rate at 2 Hours
3	1.9	0.286	0.067
6	2.9	0.187	0.035
4	6.9	0.127	0.012

Glycolysis of sperm can be measured anaerobically or aerobically with a Warburg apparatus. Comstock *et al.* (1943) found that anaerobic glycolysis of ram semen was highly correlated with respiration rate and livability of the sperm under storage conditions. Since this is true, either glycolysis or respiration alone can be used for routine testing of semen.

Mann (1948) developed a method of determining the rate of fructose utilization by sperm and has proposed it as a means of evaluating semen quality. He has found that fructose is the main carbohydrate naturally occurring in semen and present as a principal source of available energy to the sperm cells.

The methylene-blue reduction test, adapted to semen analysis by Beck and Salisbury (1943), is especially useful in rating samples of bull semen. Two-tenths milliliter of bull semen is diluted with 0.8 milliliter of yolk-citrate diluent in a small test

tube. To this is added 0.1 milliliter of a methylene-blue solution composed of 50 milligrams of methylene blue dissolved in 100 milliliters of sodium citrate buffer. When the tubes are incubated in a water bath at 45° C., the best samples reduce the blue color of the dye in 3.5 to 6 minutes. Poor samples require longer—up to 40 minutes.

4. Differentiation of live and dead spermatozoa can be accomplished by subjecting a very small sample of semen to a sodium phosphate buffer solution containing the vital stain, eosin B (Mayer *et al.*, 1951). Usually another stain such as fast green is added to give contrast. A smear of this mixture is prepared on a slide and dried rapidly. The dead spermatozoa in the sample take up the eosin stain, and the live ones remain unstained. In this way differential counts can be made. This technic is quite useful in evaluating semen quality and as an aid in developing techniques for handling semen to be used for artificial insemination.

5. Semen can be evaluated on the basis of its content of morphologically abnormal sperm. This is done through the preparation of smears of semen on a microscope slide and staining the sperm cells. A number of suitable stains and technics are available. Differential counts are then made, and the various morphological types are classified and enumerated. Males with good fertility records in the field generally have abnormal counts of less than 15 per cent.

6. It has been known for many years that there is a high correlation between the fertilizing capacity of sperm and the maintenance of sperm motility when the semen is stored at relatively low temperatures (5° C.). To determine these ratings for livability at a low temperature, a great deal of time is involved. Studies by Beck and Salisbury (1943) have shown that the length of storage time can be reduced to one to two hours by increasing the storage temperature to 46.5° to 47.5° C. The correlations for storage at these two temperatures was very high. Therefore, samples can be rated for motility before and after incubation at 46.5° to 47.5° C., and the ability of the sperm to survive at this temperature is used as a criterion of quality.

The ability of sperm to withstand temperature shock (a sudden reduction in temperature) is related to its viability (Cumings and Winters, 1953). A small diluted sample of semen is warmed to body temperature, then suddenly immersed in a vessel

of ice water and held there for 10 minutes. Good samples will show less proportional increase in dead sperm after this treatment than poor samples. The live and dead staining technic or motility ratings used before and after the temperature shock are useful measures for this test.

No single test of semen quality is adequate in itself for measuring the relative degree of fertility of a male. Recent information seems to indicate that a combination of the above tests and possibly the development of new tests to be used in conjunction with these will be more useful to accurately appraise the breeding efficiency of males. No exact scale for fertility along that line is available at present.

Unfortunately, no satisfactory comparable measure of the female's relative fertility has been developed. There is no question but that there is variation in the viability of ova; but these gametes are produced in small numbers, compared to the male, and are too difficult to recover in large enough numbers for adequate appraisal. Some recent work, however, has demonstrated variations in metabolic activity of eggs from lower forms of animals.

Artificial Insemination

Artificial insemination is the deposit of male reproductive cells (sperm cells) in the female reproductive tract by mechanical means rather than by direct service of a male. It has been known for a long time that it is possible to breed animals artificially, but the early methods were not entirely satisfactory. Only since about 1940 has the practice been expanded to any large extent in the United States. Insemination technics have been developed and improved; research has been conducted on methods of collecting, storing, handling, and evaluating semen; and associations have been formed for artificial insemination.

Uses of Artificial Insemination. In a number of ways artificial insemination is proving useful to the livestock industry. It should always be regarded as a tool for furthering constructive animal breeding.

1. The usefulness of a given sire may be greatly extended. Two advantages are: the young sire can be evaluated earlier in life than he could be by natural mating; and more extensive use can be made of sires that prove to be valuable because they can be used on more females. The progeny testing of a young sire can be done in a relatively short time, and matings can be made to a wider variety of females by using artificial insemination. It is then possible to put the males with the highest proving into a more extended regular service at an earlier age and during the peak of their fertility. Through artificial insemination the service of a bull or ram may be extended 10, 20, or more times and that of a stallion or boar 2 to 4 times. During recent years certain bulls used in artificial breeding associations have each bred as many as 2,000 to 4,000 cows annually. A single ejaculate may be diluted and divided so that several females may be inseminated. Also the number of wasted matings is reduced. A male running with a group of females will mate each female a

number of times during a single heat period. Service counts made on a vigorous ram run as high as 22 within an eight-hour period. In the same number of regulated services, the ram could have ejaculated enough semen to have inseminated 400 ewes artificially.

2. Valuable sires that cannot make a satisfactory service because of physical handicap, such as age, size, or a crippled condition, can, in many cases, be used successfully by means of artificial insemination. An example of such a male was a Shropshire ram which was owned by the University of Minnesota. Because of advanced age, the ram was unable to make a sufficiently vigorous service to deposit semen much beyond the vestibule. His sperm were fairly active, but he failed to settle the majority of the females served. When his semen was collected and used artificially, a normal percentage of ewes was settled. In another instance, a young Aberdeen-Angus bull was too short-legged to make a satisfactory service. Furthermore, his ejaculate was small, and the number of vigorous sperm cells was rather low. He settled few females by natural service, but the whole herd was settled through the aid of artificial insemination.

In crossbreeding it is often desirable to use breeds quite dissimilar in size, and difficulty is frequently encountered in making such matings. This difficulty can be overcome by artificial insemination.

3. In monogamous species and in cases of psychic incompatibility, artificial insemination can be used to advantage.

4. Matings can be made between animals located at distant points at less expense or hazard than would be incurred by transporting one of the animals. Semen can be shipped considerable distance with satisfactory results.

5. Artificial insemination properly used can be instrumental in the control of some diseases.

6. Artificial insemination is making it possible for individual farmers to dispense with their own bulls. Dispensing with bulls is a special advantage to the dairy farmer because dairy bulls are often dangerous and require valuable room, labor, and feed. Artificial insemination is proving of most value to the dairy farmer.

7. In cases of delayed ovulation on the part of the female, artificial insemination provides a means of breeding the females

after they have gone out of heat and of thereby supplying fresh semen in the oviducts closer to the time of ovulation than is possible with natural breeding. Post-oestral ovulation always occurs in the cow, and some hard-to-settle cows consistently ovulate later than is expected on the average. These individuals should be bred after they have passed out of heat, and artificial insemination is the best means of making this type of mating. Many mares also perform in a like manner.

8. Through artificial insemination dairymen and beef cattle producers located outside the range areas are better able to use crossbreeding in a more systematic order. Through centrally located bull studs they can secure semen from different breeds without having to maintain several bulls of the different breeds needed on their own farms.

Limitations of Artificial Insemination. Artificial insemination has some limitations:

1. Cost of equipment and added labor, which a few years ago limited the widespread use of artificial insemination, has since become of minor importance. The formation of artificial insemination organizations and the increased availability of instruments have almost eliminated equipment costs and any additional labor on the part of the farmer.

2. Not all inseminators are properly trained; some cannot be properly trained. This condition will probably always be a factor limiting the most successful use of artificial insemination.

3. The possibility of disseminating disease may always be present, but suitable precautions have already greatly reduced the hazard.

4. The usefulness of artificial insemination in breeding beef cattle, sheep, swine, and poultry may be limited for some time. Most beef cattle in the United States are bred on the range, and it is difficult to visualize artificial insemination as becoming generally practicable under range conditions. The relatively low cost of sires of the other three species may make artificial insemination unpractical. With swine, a boar's service can be spread to so few females that extensive use of artificial insemination is unlikely.

Cost of Artificial Insemination. The cost of artificial insemination may be calculated in two ways: in actual cash out-

lay, artificial insemination can compete favorably with most natural matings where mature bulls are used; Dowell and Winters (1942) found that the actual breeding costs by artificial insemination averaged only about one-half that of direct service by the bull.

Through the use of well-selected young sires and proved bulls, farmers, on the average, may have their cows bred to bulls of higher quality than they could or would have if they had purchased their own bulls. When this fact is taken into consideration, comparisons of actual costs in dollars have little significance, especially since the cost of artificial insemination in dollars is much less than when natural matings are made.

Proper Organization and Technics Required. Artificial insemination is a method of breeding which has the possibility of great benefit to farmers; however, a large financial loss may occur if the associations for artificial insemination are improperly organized or managed.

The individual farmer is mainly interested in two things: improving his herd and getting his cows or other females settled. If, through improper organization of the artificial insemination unit or through the use of improper technics, the herd owner's females are not successfully settled within the limits of normal expectations, the resulting financial loss may more than offset the long-time benefits. It is imperative that each step in any artificial insemination program be taken accurately and with the utmost care.

Semen. Semen is a suspension of spermatozoa in seminal fluid. It is an opaque, white to light cream-colored fluid. Some of the quantitative characteristics of semen from different males are given in Table LII.

TABLE LII. QUANTITATIVE CHARACTERISTICS OF SEMEN *

Animal	Volume per Ejaculate,			Sperm Concentration, Sperm			pH
	Cubic Centimeters			per Cubic Millimeter			
Bull	0.5	<u>5.0</u>	15.0	300,000	<u>800,000</u>	2,000,000	6.5–7.5
Ram	0.5	<u>1.0</u>	2.0	500,000	<u>2.000,000</u>	6,000,000	6.2–7.0
Stallion	40	<u>100</u>	350	30,000	<u>100,000</u>	800,000	7.0–7.8
Boar	125	<u>200</u>	500	25,000	<u>100,000</u>	1,000,000	6.8–7.2
Cock	0.1	<u>0.6</u>	1.5	50,000	6,000,000		7.3–7.8

* Underlined figures represent averages; others, the range.

Collection of Semen. Several methods of collection have been developed as follows:

1. The artificial vagina provides the most satisfactory method of collecting semen from the bull, stallion, or boar; and it may be used for the ram. Artificial vaginae suitable for bulls (Fig. 85) are easily obtainable today from well-established livestock supply companies. The vagina consists mainly of a heavy rubber casing through which a thin rubber tubing is inserted and folded over each end and fastened with rubber bands so as to form a jacket between the liner and heavy rubber casing. A thin rubber director cone is fastened over one end of the artificial vagina, and the glass semen-collecting vial is attached to the smaller end of the cone. A larger glass vial partly filled with warm water (temperature, 85°–90° F.) may be placed over the semen vial and sealed at the open end with a heavy rubber ring between the two. The latter provides warmth to the semen vessel so as to avoid a sudden drop in temperature when semen is being collected during cold weather. However, the semen-collecting vial need not be used at the time of collection; instead the director cone can be folded back over the end of the outside heavy rubber casing and the semen poured out of the vagina into a glass vial when the instrument is taken into a place of room temperature after collection. An additional aid to avoid rapid cooling of the artificial vagina during cold weather is to wrap the closed end with an electric heating pad (if electricity is available) or to use a hot water bottle in the same way.

After the artificial vagina has been assembled as outlined above and according to Fig. 85, the jacket between the inner liner and outside casing is filled with water hot enough to give a temperature inside (when checked with a thermometer just prior to collecting semen) that will be agreeable to the bull and will not injure the semen. This temperature usually averages about 105° but may vary from 95° to 115° F., depending on the bull. It was the author's experience that, when semen was collected from jacks by this method, some jacks required artificial vagina temperatures as high as 140° F. In any event, it seems quite necessary to cater to the likes and dislikes of the male being used. The pressure within the water jacket must also be adjusted to give sufficient room for the entrance of the penis and yet suitable to the likes of the male.

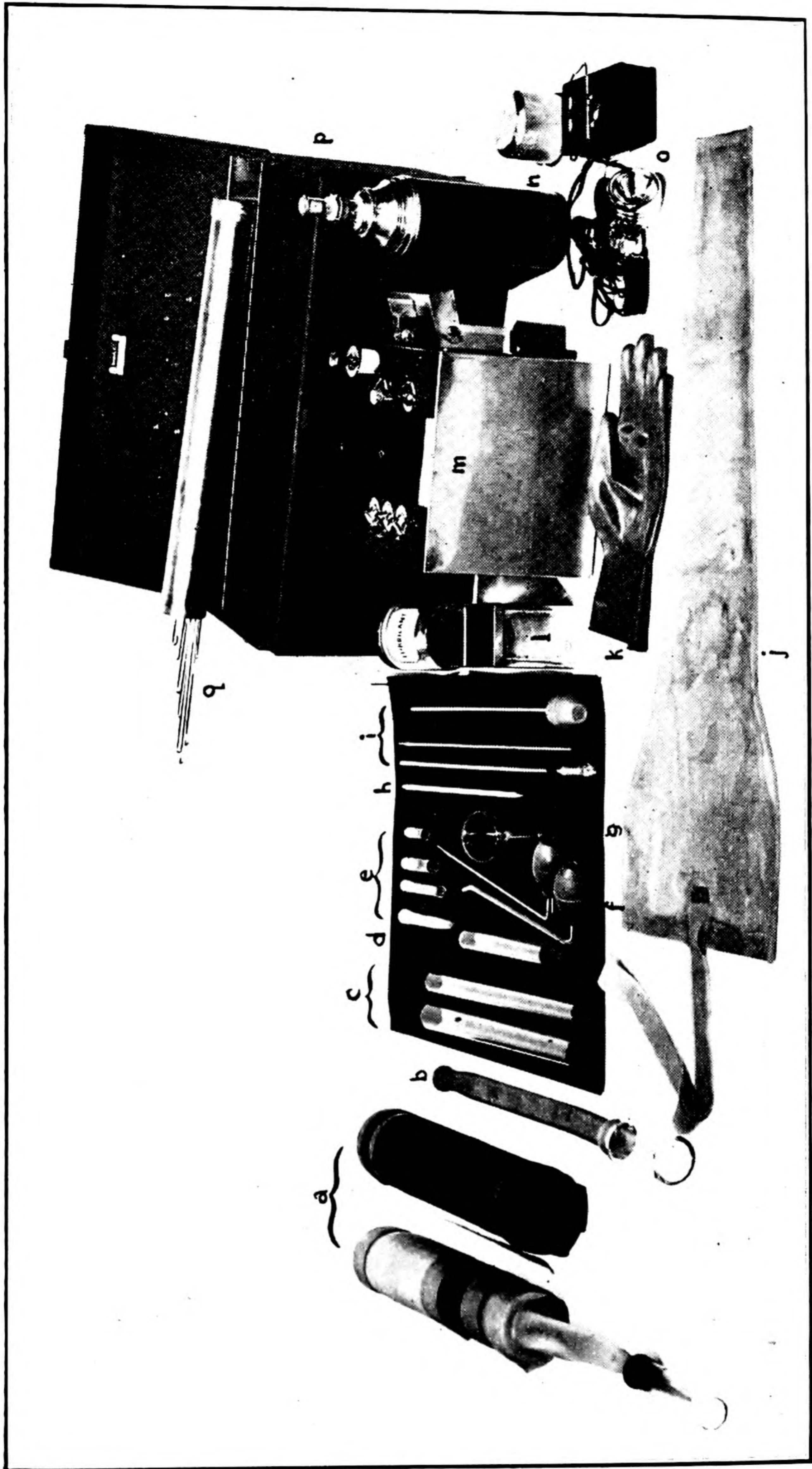


FIG. 85. Equipment used in artificial insemination. (a) Bull artificial vaginae; (b) simple type artificial vagina for a boar; (c) vaginal speculums for the cow; (d) vaginal speculum for the ewe; (e) semen vials; (f) semen-collecting pipette and inseminating pipette for sheep; (g) semen-collecting funnel; (h) thermometer; (i) inseminating pipettes for the cow; (j) rubber sleeve; (k) rubber glove; (l) small equipment tray and lubricating jelly; (m) portable refrigerator for transporting semen; (n) Thermos jug equipped for transporting semen; (o) head lamp; (p) inseminator's equipment kit; (q) inseminating pipette case.

The next step is to lubricate the inside of the vagina generously yet not to the extent that excess amounts of lubricant will flow into the collecting vial. A most suitable lubricant is one prepared as follows: (1) Mix 6 grams of powdered gum tragacanth with 10 cubic centimeters of glycerine and stir until the mixture has a creamy consistency. (2) Add 100 cubic centimeters of boiled distilled water while still hot to this mixture and beat thoroughly. (3) A small thymol crystal may be added in order to prevent mold and bacterial growth, and the mixture is allowed to stand for at least 24 hours. This lubricant should be refrigerated until needed. It is considerably better than mineral oil or Vaseline which have been used so extensively in the past, because being highly soluble in water it washes off the rubber equipment easily and it is not injurious to sperm. Mineral oil or Vaseline deteriorates rubber quite rapidly and is very difficult to remove.

The male to be used is now allowed to mount a female, another male, or a dummy. As the mounting act takes place, the operator directs the penis (by taking hold of the sheath) into the artificial vagina, and the ejaculation is made. The semen is then drained immediately into the collecting vial and taken into a room where the temperature is about 72° F. It is not allowed to go below that temperature at any point during the procedure until it has been processed for storage.

The same instrument can be used for collecting boar semen excepting that the semen is collected into a large receptacle from the director cone. With some boars a simple rubber-tubing type of artificial vagina may be used in place of the one with a water jacket (Fig. 85). It is merely lubricated on the inside and placed over the penis when the boar mounts a sow, and the semen is then allowed to flow into a large glass receptacle as ejaculation takes place. With the boar it is sometimes necessary to simulate the vaginal contractions of the sow by repeatedly squeezing the outer casing of the vagina with the water jacket.

The artificial vagina for the stallion and jack has been described in detail by Lambert and McKenzie (1940). It is larger but constructed and used according to the same basic pattern as for the bull. The one for a ram is of the same order and is described by these workers.

2. The vaginal method of collecting semen is merely allowing the male to serve a female in or out of heat naturally and then withdrawing the semen from her vagina. A female out of heat is definitely preferred because vaginal secretions during oestrus are quite detrimental to sperm. This method is most satisfactory for collecting semen from rams, mainly because a ewe out of heat can be restrained easily for the collection. However, certain males refuse to work under these conditions. Before allowing the ram to mount the female, her vagina should be rinsed thoroughly with a suitable clear semen diluter or with 0.9 per cent sodium chloride solution. After ejaculation the semen is withdrawn from the anterior end of the vagina into a glass pipette (Fig. 85). When this method is employed, both the male and female must be absolutely free from diseases.

3. Collection of semen from the bull by massaging the ampullae per rectum has been used quite successfully and particularly when the bull has been injured so that he is incapable of mounting, when he refuses to use the artificial vagina, or in certain cases when the bull is incapable of producing an erection. If proper care is taken, a bull can be used by this method regularly over a long period of time without injury to the bull or to his reproductive tract. The technic does, however, require considerable skill on the part of the operator, and in many instances a certain amount of training on the part of the bull is necessary.

The bull is first secured firmly in a suitable stanchion or stocks. The outside of the sheath should first be clipped, washed thoroughly with warm water, and carefully dried with a clean towel. During the washing process it will be found that the bull will urinate frequently. The washing should be continued until urination ceases, because urine is quite harmful to sperm survival.

An assistant then holds a small glass funnel leading to a glass semen vial directly beneath the bull's sheath. He should have several glass vials available in order to be able to change at any time during the collection if contamination of part of the sample should occur. The operator, having trimmed his fingernails quite closely and having placed a clean rubber sleeve over his arm and a surgeon's rubber glove over his hand, then inserts his hand up the bull's rectum and removes all feces present. With his hand well lubricated, he palpates the bull's genital organs lying

on the floor of the pelvis. He may next carefully massage the seminal vesicles, the prostate, and the Cowper's glands, thus

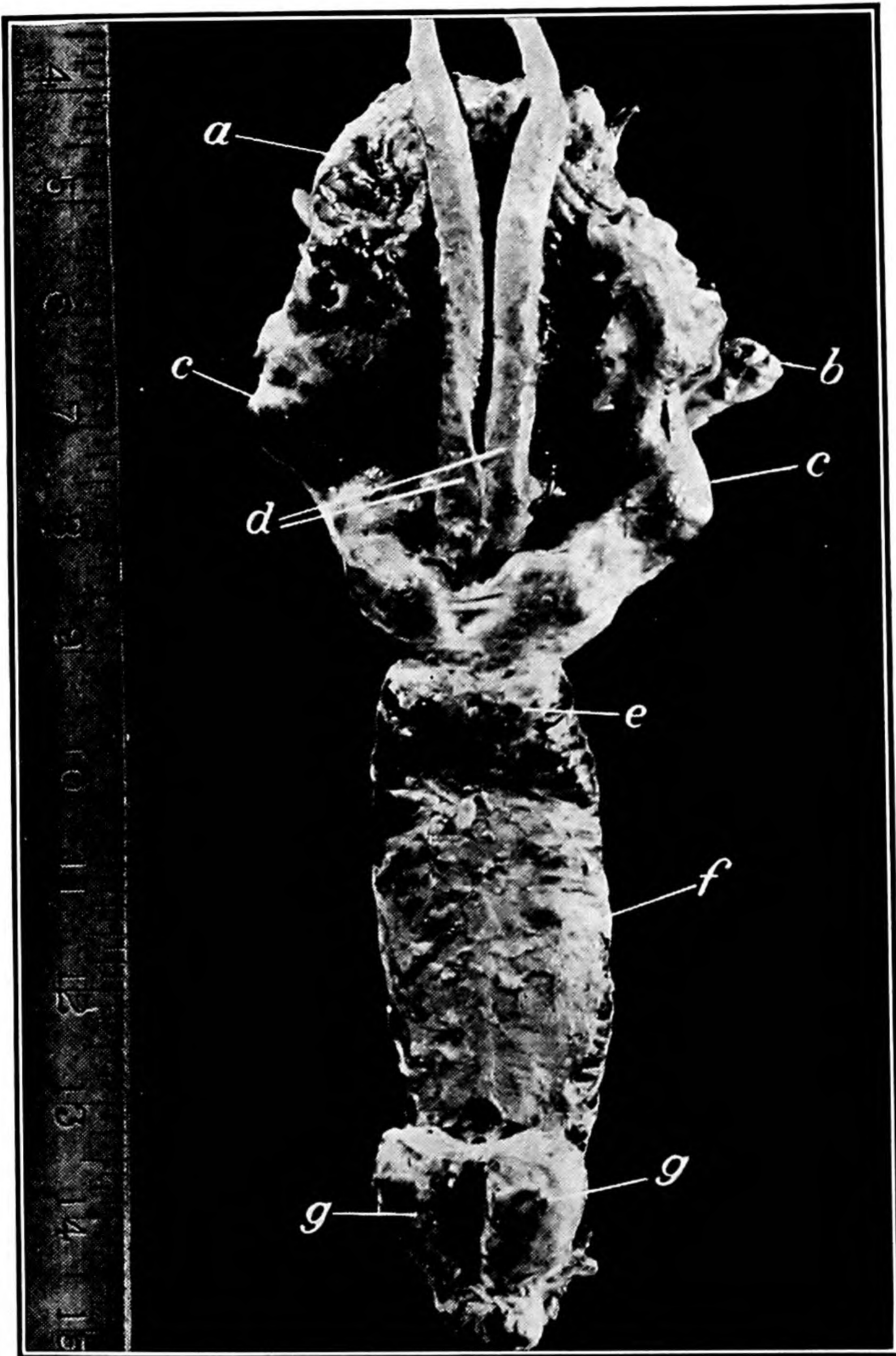


FIG. 86. Dorsal view of the internal organs of a bull. (From Miller and Evans in *Journal Agricultural Research*.) (a) Bladder; (b) ureter; (c) seminal vesicles; (d) ampullae; (e) body of prostate; (f) pelvic urethra; (g) bulbo-urethral (Cowper's) glands.

attempting to stimulate some secretion of seminal fluid to rinse the bull's urethra. Sometimes, this massage may stimulate an ejaculation of semen. If not (and generally it does not), the operator then starts pressing one ampulla at a time between the

floor of the pelvis and the first three fingers of his hand, at the same time drawing the hand backwards as if to literally squeeze or "milk" the spermatozoa out of that portion of the tract. This action is repeated several times in a rhythmic manner on each ampulla until a fair amount of semen has been recovered at the end of the penis. At no time should excessive pressure be applied.

Before attempting to collect semen by the massage method it is well to make sure that the bull has not ejaculated either by natural service or by some method of collection for two or three days to insure the probability that the ampullae are full of spermatozoa. If they are not full, the process of collection is much more difficult. The collection of semen by the massage method is considerably easier from a thin bull than from a fat one.

Semen collected by the massage method is generally not of as good quality as that collected with an artificial vagina, owing in part to the increased chances of contamination and probably also owing to the incomplete imitation of natural ejaculation.

4. Collection of semen by electrical stimulation has been used on the ram and small animals. It was first described by Gunn (1936). To carry out the operation, the ram is laid on his side with his feet and head fastened down quite securely, and a series of electrical shocks is administered to him through electrodes, one of which is placed 6 inches inside his rectum and the other between the fourth and fifth lumbar vertebrae. About ten or twelve and not more than twenty shocks are given in a series of 5 seconds on and 5 seconds off, of increasing voltage from 10 to 50 volts and an amperage of not over 150 milliamperes.

Alternating current is used by passing it through the primary of a small transformer and tapped in the secondary at the voltages required. If electric current is not available a small hand-turned magneto can be used to generate the electricity. The electrode for the rectum is prepared by inserting a heavy copper wire with a flange on the free end through a piece of glass tubing and attaching the other end to one pole from the transformer. The other electrode for the lumbar region is prepared in a similar way, and the free end is merely pressed tightly against the skin (a spot about four square inches having been clipped free of wool) directly over the spinous processes between the fourth and fifth lumbar vertebrae.

To collect the semen during the series of electrical shocks, the penis may be withdrawn from the sheath sufficiently to expose the glans penis and thus allow the semen to flow therefrom into a clean glass vial. However, it is sometimes quite difficult to hold the ram's penis during the procedure. If so, a small clean glass test tube of the right size may be inserted into the sheath with the open end covering the glans penis to collect the semen.

Semen collected by electrical stimulation is often of poor quality because of frequent contamination by urine which may also be expelled due to this type of stimulation. In addition, rams vary considerably in their response to the method. Generally, the ram is temporarily paralyzed in the hind quarters for 10 to 15 minutes immediately after the shocks have been discontinued and he has been released. This is of no serious consequence, and no permanent damage will ensue if proper precaution has been taken to avoid too many shocks or too high voltage or amperage; hence the necessity for including a voltmeter and milliammeter. It has been the author's experience also that several treatments at regular intervals 1 to 2 days apart on the same ram has no permanent damaging effects. This method should be used only after collection by natural ejaculation has failed or is not possible.

5. Upon special occasions, semen may be withdrawn directly from the epididymis and used for artificial insemination purposes. Attempts have been made to withdraw it from the live animal with a hypodermic syringe and needle, but serious complications from infection and trauma have resulted. This method is generally applied when the sire has been marketed and butchered because of some incurable injury or other cause. At that time the testicles are removed early in slaughter, and the sperm is squeezed out of several openings made in the epididymis. The sperm are then diluted with 0.9 per cent sodium chloride solution or Ringer's solution for immediate insemination or are diluted with a suitable semen diluter when it is proposed to store them for later inseminations. This method has been used on several bulls that were marketed from artificial breeding studs, bulls that had become crippled so that they were no longer useful in the regular routine of the stud yet were valuable enough as sires for the additional progeny from them to be highly desirable.

From these collections as high a percentage of conceptions has been obtained as from semen collected in the regular manner.

Care and Storage of Semen. Special care must be exercised in handling semen at all times. Sperm vitality can be lowered very easily or destroyed completely through the slightest carelessness. At no time should the semen come in contact with any materials or vessels except those recommended in these procedures from the time of collection until it has been deposited within the female tract. Some of the commonest sperm-destroying agents or conditions to which one might be apt to expose semen are: (1) any trace of cleaning agent used to clean the collecting and inseminating equipment, (2) distilled or tap water, (3) urine, (4) filth, (5) disinfectants, (6) semen diluters with improper ingredients or of the wrong concentration, (7) acid or alkaline solutions, (8) a sudden drop in temperature, (9) a sudden rise in temperature, (10) temperatures much above body temperature, (11) long exposure to temperatures above the optimum storage temperature of 38° to 40° F. (sperm has the capacity of survival for long periods at body temperature but only in the genital tracts of either the male or female), (12) freezing (particularly slow freezing), (13) exposure to a strong light (except for short duration at the time of collection or insemination), and (14) drying.

Most of the semen used for artificial insemination has to be shipped to outlying points from where it was collected, and, in dairy cattle, particularly, it is one to three days old, and sometimes as much as five days old, at the time that the cows are inseminated. This necessitates adequate methods and care in preparing it for storage and shipment. Three basic procedures to preserve the fertilizing capacity of sperm for this purpose are: (1) cooling to an optimum storage temperature of 38° to 40° F. and holding the semen at that temperature constantly until it is used for insemination, (2) the addition of suitable diluters, and (3) packaging it in the properly refrigerated carton.

The process of cooling, which is essentially the same for all species, must be gradual with no fluctuations of temperature. Immediately after collection the raw sample is put into a room of 72° F. and allowed to come down to that temperature by merely exposing the entire sample in its original collecting vial to the air. During this time it may be examined for quality. It

can then be diluted (the temperature of the diluter when added must be the same as that of the semen) at this temperature and divided into the portions to be shipped out. It is generally recommended that the shipping vials be of such a size that they can be filled to the top and all air thereby removed. Cooling from this point should be quite carefully controlled and is accomplished best by placing all filled vials in a vessel of water at 72° F. with a rack to hold the vials upright and by then placing the vessel in a refrigerator at 38° to 40° F. The amount of water should be such that the drop in temperature of the semen to 38° to 40° F. will take at least 1 hour. Not more than 2 hours are required. If, however, it is desired to cool the semen to 33° to 35° F. (this temperature can be used instead of 38° to 40° F. as an optimum), the cooling from 38° to 40° F. should take an additional 2 hours. Instead of the large vessel of water to control the rate of cooling, each vial of semen may be wrapped with several thicknesses of paper which in turn acts as an insulator.

The main factors that necessitate the cooling process are: (1) Sperm at this temperature discontinue their movement and thus conserve the energy or ability to utilize the energy with which they were supplied when ejaculated. When they are placed in the female tract, where body temperature is restored, they start moving again, provided they have not aged too much or lost their vitality from other causes. (2) At the optimum storage temperature, bacterial growth and action are inhibited. The metabolism of large amounts of bacteria in semen produces materials and conditions toxic to sperm if it is allowed to go too far.

Freezing of semen, particularly slow freezing that might occur from exposure to ordinary sub-freezing weather conditions or from merely placing a vial of semen in the freezing compartment of a refrigerator, will kill all spermatozoa immediately. However, rapid freezing accomplished by placing semen in Dry Ice (−78° C.), liquid hydrogen (−183° C.), or liquid nitrogen (−196° C.) has been shown to preserve spermatozoa for considerable lengths of time (up to 35 days for some species). This procedure does not have too much practical application as yet, except in very special cases.

Many semen diluters have been developed for the various species of farm animals. The primary purpose of diluters is to

increase the volume of the ejaculate of a male so that it may be used to inseminate a larger number of females. However, when semen is to be stored for over one hour, the semen should be cooled and a diluter should be added even though a volume increase may not be necessary. The diluter provides a buffering action which maintains a constant pH, since, without the buffer, the metabolic processes of the spermatozoa will render the medium too acid, which in turn will be toxic to sperm. In addition, many diluters provide some food for the sperm and contain materials that make it possible for sperm to withstand temperature shock to some extent.

The essential properties of a good diluter are: (1) It must not be toxic to spermatozoa. (2) The osmotic relations between the diluter and spermatozoa must be similar to those in the undiluted semen. (3) The hydrogen-ion concentration of the solution must be favorable for continued viability of the spermatozoa. (4) It should contain a buffering solution to protect against marked changes in the hydrogen-ion concentration. (5) It should increase the length of time that semen can be stored without loss of fertility. (6) It should prevent injury from cold shock. (7) It should be inexpensive and easy to prepare.

Modifications of the bull semen diluters developed by Lardy and Phillips (1939) and by Willett and Salisbury (1942) are in wide use today. The first one is an egg yolk-phosphate diluter prepared by adding one part by volume of strictly fresh egg yolk (membrane removed) to three parts by volume of a phosphate buffer prepared as follows: to 100 cubic centimeters of sterile glass-distilled water add 0.2 gram KH_2PO_4 (C.P. grade) and 2.0 grams $\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O}$ (C.P. grade). The second one is an egg yolk-citrate diluter prepared by adding one part (by volume) of fresh egg yolk (membrane removed) to three parts (by volume) of a sodium citrate solution prepared as follows: to 100 cubic centimeters of sterile glass-distilled water add 2.9 grams $\text{Na}_3\text{C}_6\text{H}_5\text{O}_7 \cdot 2\text{H}_2\text{O}$ (C.P. grade). The original formulae called for equal volumes of egg yolk and phosphate buffer or sodium citrate solution, but it has been found that 25 per cent egg yolk (by volume) is sufficient for all practical purposes. Equally good results have been obtained with either diluter. The citrate diluter has the advantage over the phosphate diluter that its use makes for easier microscopic examination. The egg yolk and

phosphate buffer when mixed produce a more cloudy appearance through which it is difficult to view the sperm.

Antibiotics in bull semen diluters have proved quite beneficial for certain bulls with low fertility records due to the fact that high bacterial contamination of the semen had occurred. Bacteria may come from the reproductive organs of the male, the artificial vagina used for collection, or the surrounding air. However, the bacterial count in semen from healthy bulls can be kept very low by sanitary measures, such as clean quarters for collection, regular grooming, and sterile apparatus for collecting. In spite of these measures, bacterial contamination is not completely avoidable with considerable differences between bulls. If harmful organisms are suspected, a complete bacteriological analysis should be made. If they are found, a clinical examination of the bull should be conducted to locate the source of infection, the bull being removed from regular collection schedule until he becomes free of the disease.

Satisfactory antibiotics and the amounts to be used are as follows:

Sulfanilamide, 300 milligrams to 100 cubic centimeters of semen diluter
Streptomycin, 100,000 units to 100 cubic centimeters of semen diluter
Penicillin, 100,000 units to 100 cubic centimeters of semen diluter

Any antibiotic may be used alone, but so far streptomycin and penicillin together in the amounts indicated have given the best results. The three drugs used in the above concentrations have no harmful effects on spermatozoa.

Bull semen can be diluted from one part semen to four parts diluter up to one part semen to 100 parts diluter, depending on how extensively it is to be used, the sperm concentration of the raw semen, and the quality of spermatozoa. Dilution rates above 1:400 have been used but with declining fertility even with excellent semen. Under the best conditions Salisbury and Bratton (1948) found that optimum fertility required between 5 and 10 million sperm as a minimum number per insemination. Some bulls may require consistently low dilutions of 1:4. There is too much variation between samples from the same bull and between samples from different bulls to safely operate an artificial breeding unit where all semen is diluted consistently at even as high a level as 1:100. It is much more economical to

add an extra two or three bulls to a stud for additional semen than to take chances on reduced fertility in the field.

A suitable ram semen diluter developed from experiments at the University of Minnesota can be prepared as follows: to 1 liter of sterile glass-distilled water add 15.4 grams $\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O}$ (C.P. grade), 3.2 grams KH_2PO_4 (C.P. grade), and saturate with CaSO_4 (C.P. grade). Another suitable ram semen diluter used by the workers of the U. S. Sheep Breeding Experiment Station of Dubois, Idaho, was the same egg yolk-phosphate diluter used for bull semen. Ram semen is generally diluted at the rate of one part semen to three or four parts diluter.

For stallion and jack semen the Missouri Agricultural Experiment Station recommends the use of the egg yolk-phosphate diluter given for bull semen except that, to the 100 cubic centimeters of sterile glass-distilled water, 10 grams of dextrose or glucose (C.P.) are added. One part of stallion or jack semen is diluted with one to three parts of this glucose-egg yolk-phosphate solution. The dilution is made immediately after collection and before refrigeration.

Berliner (1945) found the following a very satisfactory diluter for stallion and jack semen: to 100 cubic centimeters sterile glass-distilled water add 5.70 grams glucose (C.P., anhydrous), 0.67 gram $\text{KNaC}_4\text{G}_4\text{O}_6$ (C.P. grade), fresh yolks from two eggs, and 1.8 grams gelatin (one half-ounce gelatin capsule). Dilution is made at the rate of one part of semen to one to ten parts of diluter. With this diluter, a gel-like mass is formed upon cooling, owing to the presence of gelatin, and the sperm is held in a more stable state during storage and shipment. When warmed up to room temperature the mass returns to a liquid state.

Boar semen is generally not diluted since large volumes of raw semen are required per insemination and it must be used very shortly after collection. However, work at Wisconsin (Wiggins *et al.*, 1951) did show that small quantities of boar semen can be used with some degree of success.

Bonnier and Trulsson (1939) found that cock semen can be diluted without lowering fertility, provided it is used within an hour of collection. In their studies 1 cubic centimeter of semen was diluted with 9 cubic centimeters of modified Ringer's solution. The modified Ringer's solution was made as follows: to

10,000 cubic centimeters sterile glass-distilled water add 68 grams NaCl (C.P. grade), 17.33 grams KCl (C.P. grade), 6.43 grams CaCl (C.P. grade), 2.50 grams MgSO₄ (C.P. grade), 24.50 grams NaHCO₃ (C.P. grade).

Bull semen of good quality and properly handled can retain most of its fertilizing capacity when stored up to five days. However, it is not kept longer than three days in the operation of most dairy cattle artificial units. Most of the semen is used when 24 to 48 hours old, since most of the technicians in the field receive new shipments of semen from the central bull stud every day or every other day, the semen having been collected the day before. Not all semen from every bull can be stored more than three days. Longer time limits than these have been reported for special cases, but they are the exception rather than the rule in the practical application of artificial insemination.

Ram semen of good quality can be stored for two weeks. Again, longer periods have been noted, but very few inseminations have been made with that held for even two weeks. Stallion and jack semen stored for 24 to 48 hours has been used successfully for breeding. Boar semen generally cannot be stored longer than three to four hours and is therefore generally used immediately after collection. For maximum efficiency in artificial breeding it is generally a safe policy to use the semen from all species in as fresh a state as possible within the limits given above.

If females are to be inseminated immediately after semen collection, no dilution or cooling of the semen should take place. It is important, too, that the temperature of the semen in these cases should not drop below that of ordinary room temperature (72° F.).

A method of shipping bull semen used by one of the Minnesota artificial breeding centers has proved quite satisfactory. The shipping package and accessories are shown in Fig. 87. First, a triple-dipped rubber balloon is filled with water and placed in a freezer until solid. It is then removed, and a thin layer of ice ($\frac{1}{4}$ inch) is allowed to melt around the outside to form a soft cushion. The semen, having been diluted and placed in properly labeled glass or plastic vials (8 to 10 cubic centimeter capacity) is cooled in the refrigerator to the optimum storage temperature. The vials of semen are then placed next

to the rubber balloon and held tight by a strong rubber band. The balloon and vials of semen are next wrapped in heavy insulating paper sheets and placed in a cardboard box composed of three thicknesses of corrugated cardboard. Two extra pieces of cardboard are placed over the top, the flaps closed, and the

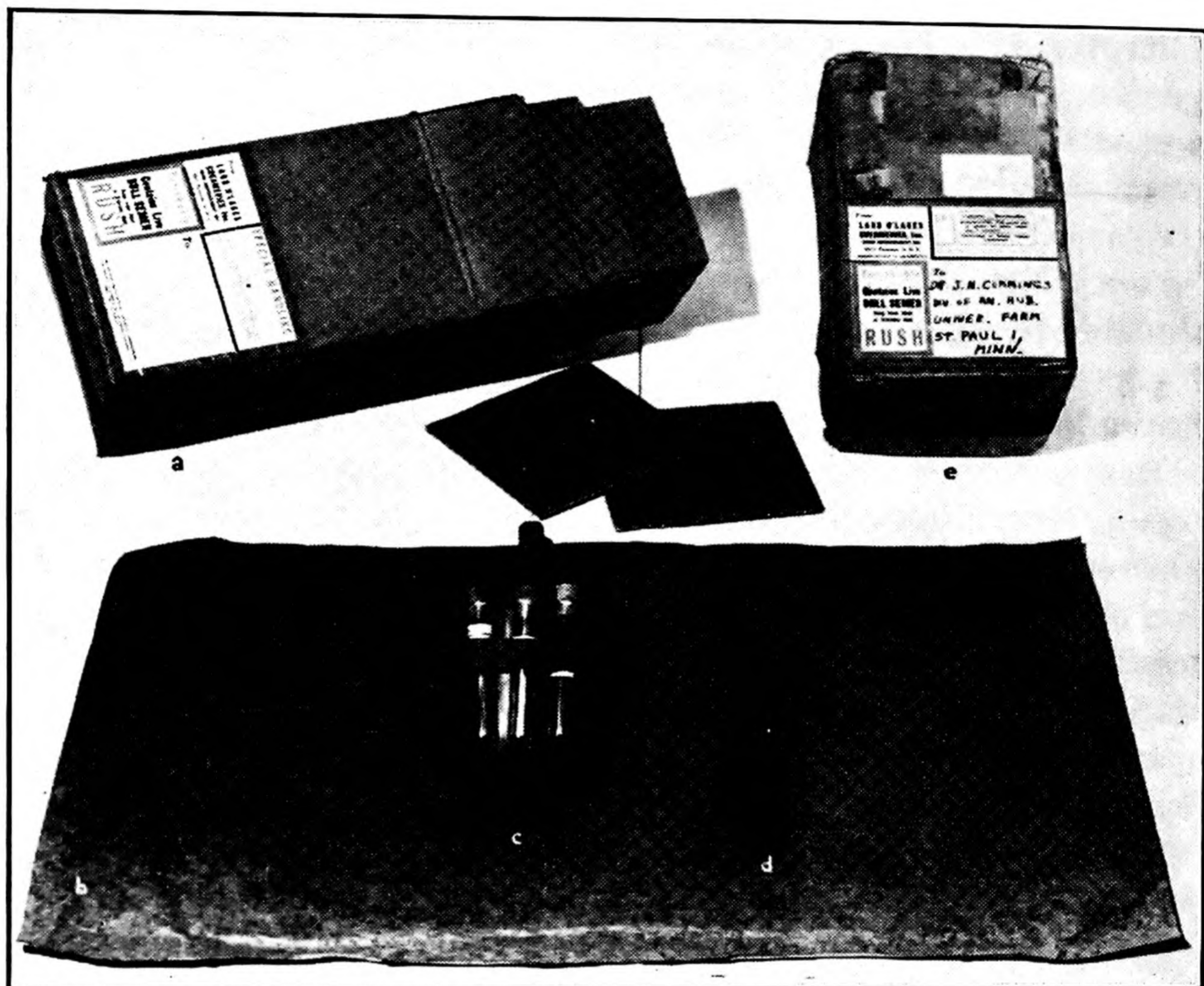


FIG. 87. Simple type refrigerator carton for shipping semen. (a) Triple-layered cardboard carton; (b) insulation sheet for wrapping semen; (c) rubber balloon filled with ice and semen vials attached; (d) rubber balloon, empty; (e) package assembled and ready for shipment.

entire carton sealed. The package is properly addressed; it is important that the following information be included on the outside: "Bull Semen. Keep in cool place but avoid freezing." It is now ready for shipment by any common carrier.

This type of shipping package provides ideal refrigeration while in transit up to about 36 hours. In any event, as long as any ice remains within the balloon and the carton has been kept sealed, the chances are good that an optimum storage temperature has been maintained. The greatest advantage of using a

rubber balloon filled with ice as a refrigerant is that as the ice melts a soft cushion is provided for the vials of semen, thus preventing breakage due to handling en route. The entire package is quite inexpensive.

Semen can also be shipped in a filled vial placed in a regular Thermos jug partly filled with cracked ice. A satisfactory arrangement is to place the vial of semen inside another larger glass tube, a heavy rubber ring between the two at the neck, and another rubber ring between the outer tube and the neck of the Thermos jug. The rubber rings fit the glass tubes into the Thermos snugly and tend to prevent breakage (Fig. 85).

As soon as a shipment of semen has reached its destination, the package should be opened and the vials of semen placed in a refrigerator operating at 38° to 40° F. If all the ice has melted, the advisability of using the semen may be doubtful unless checking it for motility proves otherwise.

Semen Evaluation. The best single appraisal of the semen from a male is the conception rate obtained when it is used on a large number of females; however, some seriously low conception rates might be avoided if the semen is properly appraised before use. A number of laboratory methods for evaluating semen quality have been discussed separately and collectively in the preceding chapter. Under routine operations of artificial insemination in the field there is ordinarily only enough time to run a few of the most rapid tests that do not require elaborate equipment or specialized skill. In any event, any semen used for artificial insemination should be checked by some fairly satisfactory technic.

Recent work indicates that the best single method of evaluating bull and ram semen is by the Rothschild spermometer to determine the rate of impedance changes (Cummings and Winters, 1953). Although this method measures the degree of motility in concentrated semen, it is more objective than microscopic examinations and eliminates the human error involved. It can be used as rapidly as microscopic examinations in the routine procedures of semen collection at the large artificial breeding centers. This method has been described and discussed in the preceding chapter.

In the past microscopic examination for motility has provided the best single appraisal of semen quality before the semen is

used. Good motility is indicated in dense semen, such as that from the bull or ram, by a vigorous swirling action as seen without a microscope and when the entire freshly collected sample is examined by holding the vial up against a strong light. This action is due to large masses of spermatozoa moving in irregular currents. However, motility appraisal should not be confined to this technic alone. A small portion of the fresh sample should



FIG. 88. A vigorous swarm of ram sperm.

be diluted with a large amount of 0.9 per cent NaCl solution or the clear citrate solution, a drop placed on a microscope slide, covered with a small cover slip, and examined microscopically at $100\times$ to $400\times$ magnification. The dilution of the examined portion should be great enough so that individual spermatozoa can be studied. Naturally the better samples will show a higher proportion of sperm moving in a straight line, at a rapid rate, and with little wasted motion. At the same time the relative proportion of motile to immotile sperm can be estimated. All too often erroneous appraisals are made of sperm motility by having too concentrated a sample on the slide. In these cases, one has a tendency to overrate sperm motility. All samples showing no motility, no progressive motility, or a low percentage of progressively motile sperm should be discarded.

Semen samples that have been stored or shipped to outlying points should be checked for motility before they are used, regardless of the length of time that they have been stored. It is often found that some samples will not stand up under storage even for short periods. An adequate microscope should be standard equipment in every breeding association stud and in each technician's laboratory. In checking semen for motility after it

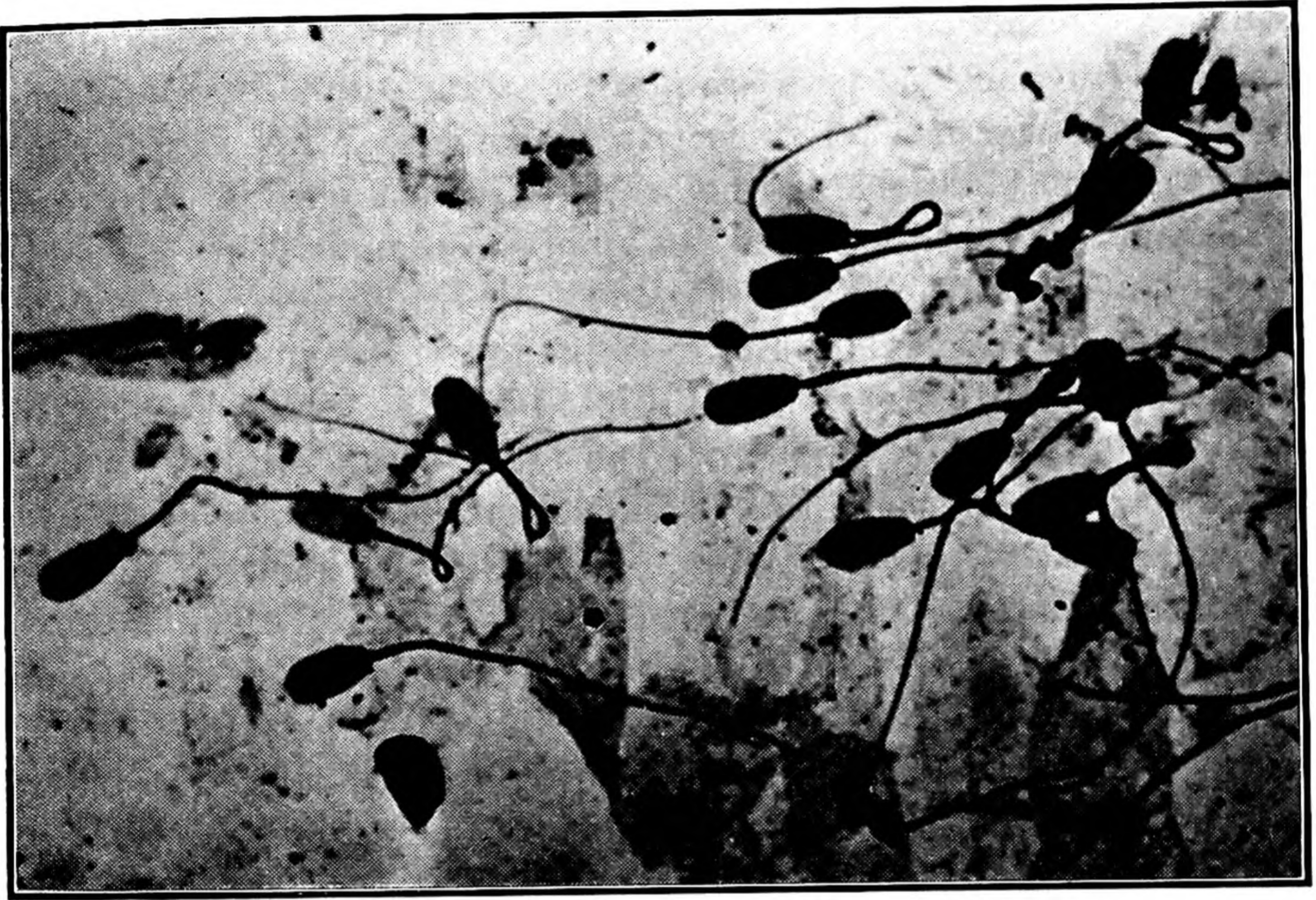


FIG. 89. A defective group of boar sperm.

has been cooled and before it is to be used, only a small portion should be removed from each vial and warmed to room temperature for examination purposes. The rest of the contents must be kept at the storage temperature. Technicians should always check the motility of semen samples held for longer periods of time than is usual.

Sperm concentrations of all samples can be adequately evaluated for all practical purposes in the routine operations of an artificial insemination center by the mere macroscopic examination of those samples in a fresh state or by microscopic examination of a small portion diluted to a constant ratio. Anyone with experience in handling semen will become sufficiently proficient in judging the sperm concentrations. Of practical impor-

tance in routine breeding operations is sound judgment of the rate of dilution that might be applied for each particular sample, particularly in avoiding high dilution rates for samples with relatively lower concentrations. It must still be remembered, however, that semen characteristics other than concentration must also be taken into consideration when rates of dilution are being determined.

Routine checking of sperm concentrations is done by counting diluted sperm with the aid of a hemocytometer counting chamber, by comparisons with standard barium sulphate suspensions, and by the use of a photoelectric colorimeter. The simple clinical type of photoelectric colorimeter which can be purchased from most scientific apparatus supply companies provides the fastest and most accurate method of determining concentrations. Standard curves can be calculated for these instruments. A small portion of fresh semen is diluted with a clear sodium citrate solution at a high enough rate constant for all samples to form a very thin suspension. A dilution rate of 0.08 cubic centimeter of semen to 15 cubic centimeters of the citrate solution has been used satisfactorily for bull and ram semen. This mixture is placed in a special vial (cuvette) in the chamber of the instrument, and the amount of light transmitted through the suspension is then measured in contrast to the amount transmitted through the solution with no semen—the more light transmitted, the weaker is the suspension and consequently the lower is the sperm concentration in the original sample. The clinical type of photoelectric colorimeter can be operated with a storage battery or from a regular 110-volt a-c line. It is relatively inexpensive and, when used regularly on most of the semen collected, more than pays for itself in saving time for this operation.

One semen test that can be used easily and at regular intervals in the stud of an artificial breeding association is to check the livability of semen samples after storage at temperatures of 38° to 40° F. or at 46° to 47.5° C. The former needs no additional equipment and is accomplished by taking motility ratings at 2-day intervals on a portion of the diluted semen from each sire used. The length of time that the sperm remain motile is a good indication of its viability and also is a means of checking the storage ability of semen. Incubation at the higher temperature (46° to 47.5° C.) will require a special incubator or water

bath operated at that temperature. However, the incubation time required is only 30 minutes to an hour, and the motility after that period as compared to the motility prior to incubation gives a good index of the livability of spermatozoa under storage.

Live and dead counts and abnormal counts made from stained semen smears are also useful routine checks on males maintained for artificial insemination.

Color and odor of semen should be checked after each collection. A tinge of red or brown color in the semen sample is due to the presence of blood, which indicates an injury or possible infection in the reproductive tract of the male. In such cases he should be checked thoroughly as to the cause, and in all cases such semen should be discarded. Odors due to putrefaction will develop in semen when allowed to stand too long at warm temperatures or even held at storage temperatures for too long a time. If strong putrid odors are apparent, the chances are good that the sperm have deteriorated beyond their useful stage.

Other semen tests and their relative values have been discussed in the preceding chapter as well as the ones mentioned here again. They are good tests but too time consuming or require too elaborate equipment to be used routinely in the practice of artificial insemination. However, some should be applied at regular intervals of perhaps once a month or once every two months on sires in regular service, as checks to avoid use of these sires in case of a slump in semen production, which may be temporary or permanent. Research work under way at the present time seems to indicate that relative fertility of a male can be predicted from the results of a series of semen tests. The work also points strongly to the possibility of having semen shipped to a central laboratory where it can be tested with more elaborate apparatus than is feasible to provide at each stud. When this is done it will be possible for artificial breeding centers to have their sires tested regularly and also, by merely sending semen samples to a central laboratory, have new sires checked before adding them to the stud.

Insemination. Much of the success of artificial insemination depends upon breeding the female at the optimum time during her oestrus period. In order to insure maximum opportunity for conception to take place, a fresh supply of a large number of viable spermatozoa should be available in the upper limits of

the Fallopian tubes of the female at the time ovulation takes place. The exact minimum number required varies with species, with matings, and particularly with semen samples used, whether by natural or artificial service. In any event, there is a definite safety in large numbers. Wasting semen should always be avoided, and it is preferable to divide the semen into portions close to the number of services anticipated by regulating the dilution rate rather than by increasing the volume inseminated, provided, of course, the dilution rate has been kept within the limits given above.

The optimum time during the oestrus period for artificial insemination and the amount of semen recommended per dose for various classes of farm animals are given in Table LIII.

TABLE LIII. OPTIMUM TIME OF INSEMINATION IN RELATION TO OESTRUS AND RECOMMENDED DOSES OF SEMEN TO BE USED

Animal	Optimum Time to Breed during Oestrus	Volume of Diluted or Undiluted Semen per Artificial Insemination
Cow	6-24 hours after onset	1-1.5 cc.
Ewe	During last half of oestrus, or, if feasible, at 12-hour intervals as long as in oestrus	0.1-0.2 cc.
Sow	During second day of oestrus and again on third day, if sow continues in oestrus that long	50-100 cc.
Mare	Repeated inseminations: on third day of oestrus and again every other day as long as mare stays in oestrus	10-20 cc. during regular oestrus 20-40 cc. during foal oestrus

Two good methods of inseminating cows artificially are: (1) the speculum method and (2) the rectal method. The equipment for both methods is shown in Fig. 85. In preparing the cow in either case, her external genitalia should be cleaned and dried. A light swabbing with alcohol as a means of disinfection is also sometimes desirable.

In the first method a glass speculum (a simple glass tube $1\frac{1}{2}$ inches in diameter and 12 to 14 inches long, the glass edges at each end having been rounded in a flame) is lubricated with mineral oil, Vaseline, or glycerine-gum tragacanth jelly and then inserted into the vagina. With the aid of a head lamp or small

fountain-pen-type flashlight (Fig. 92) the cervix is located, the opening of the speculum having been placed right around the

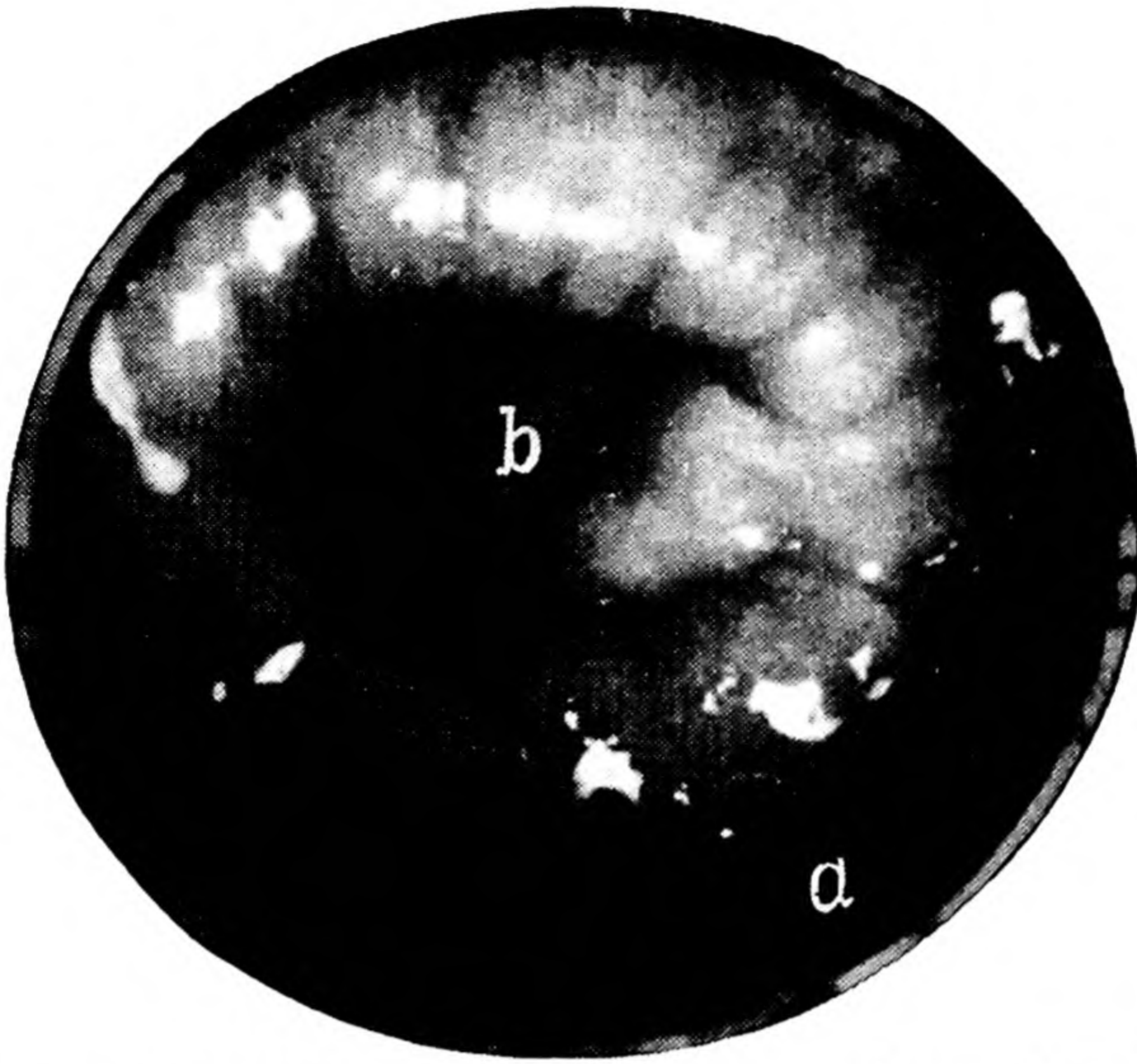


FIG. 90. Cow cervix as observed through speculum. (a) Speculum; (b) cervix.

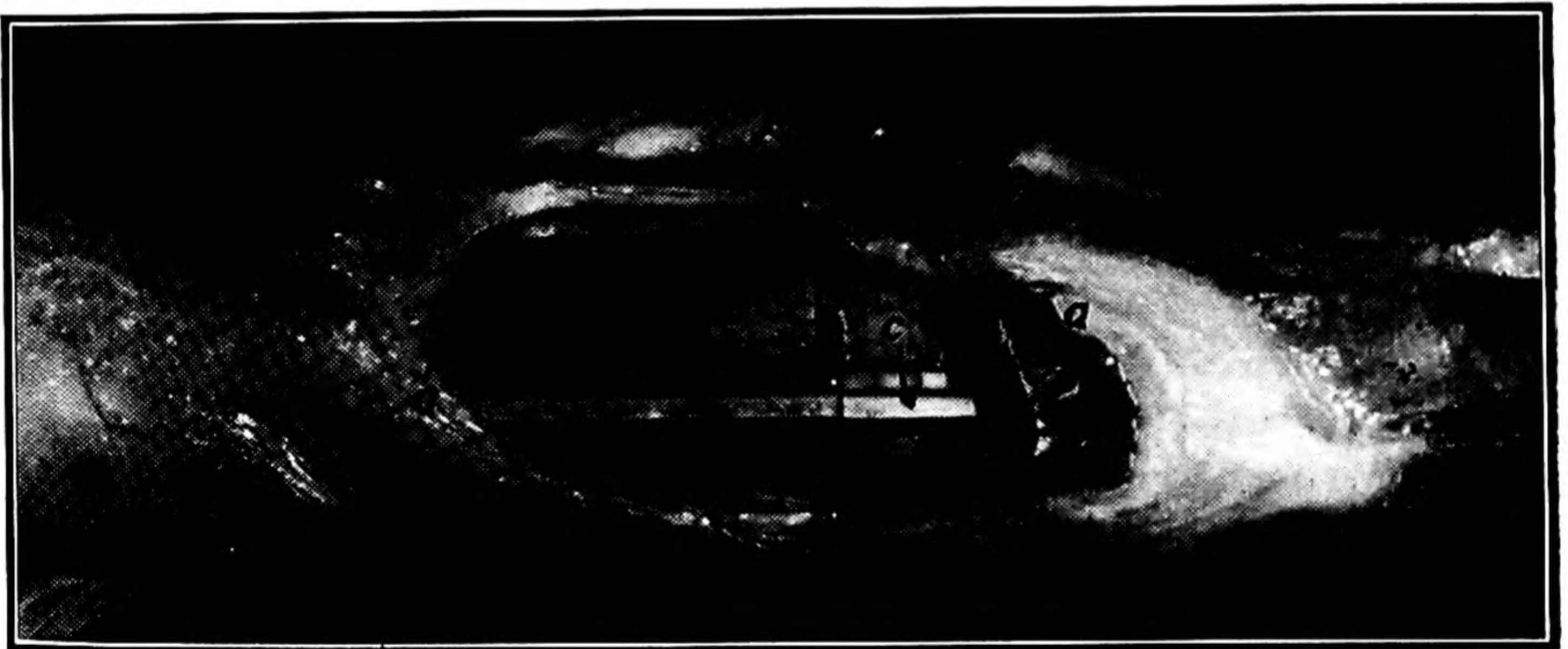


FIG. 91. Illustration of use of speculum in cow and position of instruments at the time of discharge of the semen. (a) Wall of vagina cut away; (b) speculum; (c) inseminating pipette containing semen placed in cervix; (d) cervix.

cervix (Figs. 90 and 91). The semen is deposited by first drawing 1 to 1½ cubic centimeters of the sample to be used into a clean inseminating pipette, inserting the pipette through the channel formed by the speculum with the end entering the cervical canal, and then applying pressure to the semen, forcing it

into the cervical canal or near the mouth of the cervix in case the latter is too tight (Fig. 91). Inseminating pipettes can be either glass or plastic. The latter have been used quite extensively in recent years and can be made cheaply enough so that each can be discarded after using it once, thereby eliminating



FIG. 92. The speculum in place, the cervix located by means of the headlight, and semen being placed in the mouth of the cervix. (From Herman and Madden.)

the tedious job of washing and sterilizing before using the pipette again. The pipette, whether glass or plastic, should be about 14 to 16 inches long, $\frac{1}{4}$ inch in outside diameter, with a $\frac{1}{16}$ -inch bore, and tapered at the end to be inserted into the cervix. Either a large rubber bulb or a 2-cubic-centimeter glass syringe (with an adapter and short piece of connecting rubber tubing) is attached to one end in order to draw the semen into the pipette and to expel the semen into the cervix. Or an even better arrangement is to use a small rubber bulb of only 1 to $1\frac{1}{2}$ cubic centimeters capacity. This allows the operator to draw only

the correct dose of semen into the pipette with total expression and release of the bulb and to deliver the semen into the cervix without expulsion of air. Figure 85 shows these pipettes assembled in various ways.

It is absolutely essential that a separate, clean, sterile set of instruments be used on each female inseminated, regardless of species or method of insemination. After the operation the plastic pipette is discarded, and all glassware is placed in a separate container marked: "Dirty Equipment." These pieces are then returned to the laboratory, washed, and sterilized before being used again.

Caution should be observed in depositing the semen in the cervix, regardless of method. It has been found from experience that females (particularly cows and ewes) vary considerably in the degree of relaxation of the cervix during the oestrus period. With some, this organ is sufficiently loose so that the pipette can easily penetrate the opening and the semen can be deposited inside the canal and occasionally in the uterus. The latter cases are quite rare. On the other hand, the cervix may be so tight that penetration with the pipette is difficult. If that situation is found, the semen should be left in the lips of the cervix at the vaginal opening. If the pipette is forced through a tight cervix, a great deal of damage due to trauma or infection may result. In addition, it has been found that, if the cow happened to be already pregnant and if the cervix is opened, abortion will take place. In general, it might be said: "Take it easy, and do not force anything!"

Artificial insemination of a cow by the rectal method is shown in Fig. 93. By this method the technician first places a rubber sleeve over one arm and a light surgeon's rubber glove over the same hand up to the sleeve. Some sleeves have the glove attached. He then lubricates this arm and hand well, inserts it into the cow's rectum, and cleans out the feces present. With his hand in the rectum he grasps the cervix and with his other hand inserts a clean pipette filled with semen into the vagina, guiding it along to the mouth of the cervix. The open end of the pipette is inserted into the cervical canal, and the semen is deposited there. Most technicians feel they are better able to direct the pipette into the cervix by this method since they are able to massage the organ with the hand in the rectum, thus

making it more pliable. However, the tendency is to force the end of the pipette directly into the uterus more often than should be done.

The speculum and rectal methods have given equal results in the field. Both have advantages and disadvantages; some technicians are able to use one method better than the other one.



FIG. 93. The hand is placed in the rectum and grasping the cervix. Catheter containing 1 to 1½ milliliters of semen being introduced into vagina and hence through cervix for semen depositions. (From Herman and Madden.)

Mares are generally bred artificially with the use of a gelatin capsule. The procedure is as follows: (1) Wrap the mare's tail with a piece of gauze or toweling. (2) Wash her vulva with clear water and disinfect the external genitalia with alcohol. (3) The inseminator then washes his hands thoroughly with soap and water after his finger nails have been trimmed closely. (4) He then rinses his hands and arms several times in clean water and dries them. (5) His hands and arms are now disinfected with alcohol. (6) He fills a ½-ounce gelatin capsule with semen and lubricates his arm with a sterile lubricant. (7) He inserts his hand (holding the filled capsule) into the mare's vagina and

places the capsule through the cervix into the uterus. The cervix nearly always dilates sufficiently for this operation in the mare during her oestrus period. The sanitary precautions are especially important since the mare is highly susceptible to infectious diseases of the uterus.

To breed sows artificially a 50-cubic-centimeter syringe with a glass barrel is attached to an 18-inch rubber pressure tubing (inside diameter, $\frac{3}{16}$ inch, outside diameter, $\frac{9}{16}$ inch) that is tapered at the open end. The syringe and tube are filled with semen, and the tube is then worked through the sow's vagina so that the open end enters the cervix. The semen is now expelled through the cervix and into the uterus.

Ewes are bred artificially by the speculum method. The ewe is first fastened securely in a breeding crate, which is a crate with stanchions at the head end and sides, set 10 inches apart, one of which swings on hinges and is to be used to squeeze the ewe over against the other side tightly. A clean speculum (simple glass tube 1 inch in diameter and 8 inches long with the edges of the open ends fire-polished) is lubricated and inserted into the ewe's vagina to expose the cervix in the same manner as that used on the cow. Again with the aid of a head lamp, semen is deposited in the mouth of the cervix with a 1-cubic-centimeter graduated pipette attached to a rubber bulb. This pipette may be bent at a 60° angle 3 inches from the blunt end. It is even more difficult to penetrate the cervical canal in the ewe than the cow. Generally the semen must be left in the lips of the cervix.

In inseminating females with stored semen it is possible to warm the semen rapidly without injury to the sperm. Most technicians draw the cold semen from a vial that is carried in a portable cold-temperature chamber (Fig. 85) and insert it directly into the female tract. This sudden increase in temperature does not do it any good but certainly is not as harmful as a sudden drop in temperature. The main thing to watch in regard to temperature of the semen at the time of insemination is that it does not fluctuate.

A satisfactory equipment case for field technicians is shown in Fig. 85. It has racks for all the necessary inseminating equipment for cattle and a portable refrigerator to carry the semen en route at the regular storage temperature. The latter is a

heavily insulated water-tight box with chambers for semen vials. The large chamber is filled with cracked ice, and the tubes of semen taken from a storage refrigerator or shipping carton are placed in the small chambers. A Thermos jug partly filled with ice may also be used to carry the semen in the field.

Sanitary Precautions. Exacting sanitary precautions must be taken or artificial insemination may prove more of a liability than an asset. The males should be examined by a competent veterinarian at regular intervals and pronounced free from disease. The operator must keep himself and his clothes clean at all times. He must never relax any sanitary precaution at any time. The following suggestions are recommended:

1. Glass instruments should be used wherever possible.
2. Two instrument cases should be carried by the inseminator, one for clean equipment and one for dirty equipment.
3. Clean instruments must be used for each animal.
4. Glassware should be washed as follows:
 - (a) Rinse with cold, then hot water.
 - (b) Place in cleaning solution for at least 10 hours. (This will both clean and sterilize. The solution is made by saturating tap water with potassium bichromate and slowly adding an equal volume of concentrated commercial sulphuric acid. The solution should be discarded when it becomes greenish in color. Metal instruments will not withstand the action of this solution, and for that reason the author prefers glass.)
 - (c) Place instruments in running water for at least 1 hour.
 - (d) Rinse instruments in a 1 per cent solution of sodium bicarbonate.
 - (e) Rinse with distilled water.
 - (f) Place in an oven to dry.
 - (g) Wrap instruments in paper or clean towels until used.
5. Rubber materials should be scrubbed with a paste of sodium bicarbonate and water as previously described and dried well between periods of use.
6. Rubber goods should be disinfected by dipping in chlorine water, 70 per cent ethyl alcohol, or boiling water immediately after washing; the chlorine solution must be washed from the rubber before it is set aside to dry.

7. Mineral oil and Vaseline are quite detrimental to rubber and are almost impossible to remove entirely at the time of washing. Glycerine-gum tragacanth jelly is recommended instead, for it is highly soluble in water and allows increased opportunity for keeping the equipment in a clean condition.

The new detergents have been used extensively in place of the cleaning solution recommended above. They do not, however, clean the glassware as thoroughly but are less time consuming. If they are used it is cautioned that the cleaning solution be kept on hand and used on instruments that are not cleaned thoroughly with the detergents. In addition, the detergents do not have as high disinfecting qualities as the cleaning solution, so that when they are used the glassware must be disinfected by heating in an oven 350° to 400° F. for an hour or they may be placed in a steam autoclave at 15 to 20 pounds pressure for 15 to 20 minutes. At no time should instruments be used that show cloudiness or dried residues on surfaces that will come in contact with semen.

Sire Management. Sires used for artificial insemination should be given the best of care. The young bull needs to be fitted for a long, fertile life. The proved sire often is on the decline in degree of fertility and physical vigor; hence his useful life needs to be extended as long as possible. As a rule a bull will be used more regularly when owned by an insemination association than when used for natural service.

Sires should be treated as individuals rather than as groups because of the large amount of variation between sires in their response to care and feed. In general, roughages should not be fed to the point of causing paunchiness. The ration should be adequate not only in amount of nutrients and balance between protein and carbohydrates but also in the supply of minerals and vitamins. The sire should not be allowed to become fat, and he should be exercised regularly. Each sire should be examined regularly by a qualified veterinarian for the presence of diseases such as tuberculosis and brucellosis.

Branton *et al.* (1947) recommend daily feeding of 1 pound of good-quality hay (mixed hay containing 10 per cent legumes) plus 0.4 to 0.5 pound of concentrate mixture per 100 pounds live weight to dairy bulls used for artificial insemination. The concentrate mixture should be made up of common feed stuffs suit-

able for dairy cattle and should have 12 per cent protein. Apparently no special protein need be added for semen production.

The amount of exercise for bulls in an artificial breeding stud seems to be a much disputed point. For the long-time program, however, each bull should be forced to exercise at least 15 minutes each day in order to maintain himself in a sound condition, even though it has been experienced in some places that a tem-

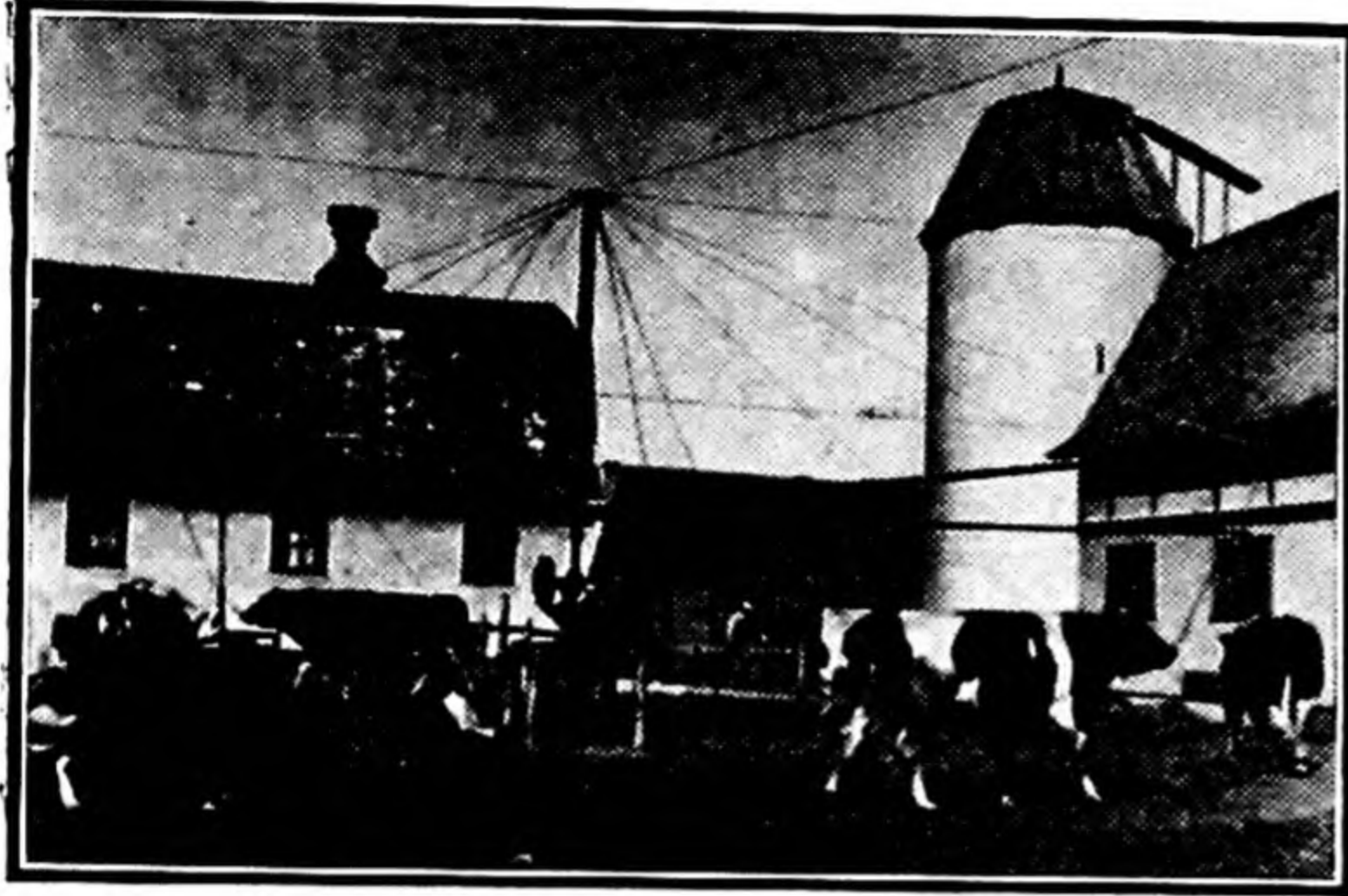


FIG. 94. Regular exercise is of importance to the well-being of the breeding bull.

porary discontinuance of exercise had no immediate effect.

Scheduling collections from bulls in studs can be varied with each individual, depending upon his own capacity. On the average, most studs find that maximum semen production can be accomplished by collecting once every five to seven days

from the same bull. There are some that have to be extended to once every two weeks.

Artificial Insemination in Fowl. The methods developed for collecting semen from the cock are quite similar to those used for larger animals; they consist of (1) placing a dish between the cock and the hen, (2) using an artificial vagina, (3) mating a hen and drawing the semen from the cloaca by means of a pipette or spoon, or (4) stimulating ejaculation by manipulation of the male. The last-mentioned, first described by Burrows and Quinn (1935 and 1937), is most widely used.

The bird may be held in a specially constructed holder or it may be held in the operator's lap. For a right-handed operator, the cock's legs are placed between the operator's left arm. The thumb and last two fingers of the right hand are placed on the sides of the abdomen as shown in Fig. 95. Ejaculatory responses are induced by rapid massage of the abdomen between the gizzard and the pelvic bones. The thumb and fingers of the left hand are so placed (Fig. 95) that the semen may be "milked" at the time of excretion. The semen is caught in a small funnel which either has a solid glass stem or has the stem filled with

paraffin. The upper portion of the funnel should also be coated with paraffin to insure the greatest recovery of semen. The funnel is held in the right hand.

Contamination of the ejaculate may be prevented or lessened by withholding food and water from the bird for 12 hours prior to securing the sample and by placing a small amount of absorbent cotton in the anterior portion of the cloaca before collection. As with the bull, the animal works better after he has been trained.



FIG. 95. Position of hands and seminal discharge during collection from the cock. (From Green and Winters.)



FIG. 96. Position of syringe placed in reproductive opening prior to insemination of the hen. (From Green and Winters.)

The amount of semen secured from the cock ranges up to 2 cubic centimeters, but the average amount per day is about 0.2 to 2.0 cubic centimeters. Pigeons and doves average from 0.01 to 0.02 cubic centimeter per collection, and turkeys 0.3 to 0.4 cubic centimeter. About 0.05 to 0.1 cubic centimeter of semen is needed per insemination.

The semen is drawn into a pipette or medicine dropper; the hen's cloaca is everted, and the opening of the reproductive tract into the cloaca is located. The pipette is inserted about one or two inches into the reproductive tract (Fig. 96), and the cloaca is allowed to return to a nearly normal position before the semen is deposited. Fowl semen may or may not be diluted with saline solution and stored at 33° to 35° F., but it is best to use the semen as soon as possible after recovery. For best results the hen should be inseminated twice a week, although satisfactory results may be secured by weekly inseminations. Sanitary pre-

cautions similar to the ones noted in connection with larger animals should be observed.

Records. If artificial insemination is to be used most successfully and usefully, careful records must be maintained. It should always be kept in mind that the foremost reason for using artificial insemination is that it is a tool for animal improvement.

Efficiency of Artificial Insemination. If proper technics are used artificial insemination is just as efficient as, and in some cases more efficient as a method of settling females than, natural breeding. Some dairy cattle associations breeding several thousand cows in a year have reported efficiencies slightly over 70 per cent for the entire year (efficiencies based on the 60 to 90 day non-returns). The over-all efficiency may be higher than that for natural breeding because so few reliable records are available for natural breeding.

Building Superior Germ Plasm

The ultimate objective in constructive animal breeding is the building of superior germ plasm. An objective in this chapter is the bringing together of fundamentals presented in previous chapters and the discussion of their applications to improvement by breeding.

The individual's heredity arises from the genes inherited from its two parents. The breeder cannot make new genes; he must work with the genes already in existence or those that may arise by chance mutation. Neither can the breeder merely mass germ plasm; the zygote has the diploid number of genes and the germ cell has the haploid number; hence as new genes are added old ones are eliminated. If the genes added are superior to those replaced the results will be constructive, but, if the choice of genes is left to chance, the results will be those of chance. Since the individual can possess only the diploid number of genes and since the breeder cannot make new genes, the constructive breeder's job becomes one of sorting the more desirable genes from the less desirable and of putting the more desirable ones in better working combinations.

In some instances the elimination of lethals appears to be of major importance in constructive animal breeding, but in the author's experience the elimination of lethals has been of minor importance in comparison with the separation of the more desirable genes from the less desirable and with putting those saved in better working combinations. There can be little doubt that the emphasis to be given different phases of the application of genetics will vary with the genetic material on hand. Here the art of animal breeding becomes of importance. The breeder who can adjust his tactics to meet the problem at hand will be more

successful than the breeder who is equipped merely with the science or the art of breeding.

The first step for a constructive breeder is to gather as much information as possible about the stock to be improved. He is then in a better position to decide in what respects the stock is to be improved. Before that question can be answered satisfactorily the breeder needs to know the strong and weak points of the strain with which he is working. For this reason detailed records of the points considered most important in the stock must be gathered carefully. The records are useful as a guide to improved selection because they bring out the strong and weak points in the breed or strain concerned. A breeder may get lost in a maze of records if too many records are gathered. It is far better to concentrate on a few of the most essential records and to gather them as accurately as possible. The only reason for raising commercial livestock is for production; hence the records of performance are of practical importance.

The fundamentals of record keeping are essentially the same for all classes of livestock, but the details naturally vary.

In the preparation of this chapter the author has drawn heavily on his own experimental results. In the first place, he wishes to give the student the philosophy of animal improvement that he has gained from his experiments, and in the second place, he is naturally much better acquainted with his own work than with others' results.

Artificial Insemination. Artificial insemination is having a marked influence on dairy cattle breeding. On the one hand, it enables commercial dairymen to utilize more fully the advantages of better sires than was possible through individual ownership of bulls. This is constructive. An increased potential production per dairy cow will result. On the other hand, artificial insemination has already markedly reduced the demand for dairy bulls. This has the effect of reducing the advantages of raising purebred dairy cattle in the hope of selling better bulls at substantial prices. Coupled with this movement is the interest on the part of commercial producers in crossbreeding. The experiments conducted by the Bureau of Dairy Industry have clearly demonstrated that there is an advantage in crossbreeding dairy cattle for productive purposes. As time goes on it is inevitable that the commercial producers will turn to crossbreeding as a

means of producing replacement heifers. Crossbreeding does not reduce the number of sires required. It does, however, reduce the number of purebred animals produced. Many breeders are maintaining their purebred herds because they believe that breed purity is an indication of superiority and because they hope for sales of purebred bulls and heifers as a means of supplementing their dairy income. It appears that the long-time effect of crossbreeding, coupled with artificial insemination, will reduce materially the number of registered dairy animals.

There is no sound reason why the dairy industry or any other phase of the livestock industry should support more purebred herds than are required for sound commercial production. On the other hand, commercial livestock production has always been and always will be dependent on an adequate supply of superior breeding stock, the germ plasm of which can be kept flowing into the commercial industry.

To date the livestock industry of this country has been dependent upon the standard breeds as the nucleus for genetic improvement. The large number within the various breeds, in itself, has allowed for considerable selection so that commercial producers have so far had the option of securing reasonably satisfactory sire replacements at quite reasonable prices. If, however, the future trend of the industry is such as to make the production of this basic seedstock unprofitable, in the end the commercial industry will suffer. For this reason it is highly important that the dairy industry begin to make plans for the maintenance of an adequate supply of superior germ plasm. Because of the factors mentioned above, it appears that this is far more likely to prove critical at an early date with dairy cattle than with any other class of livestock.

On the other hand, artificial insemination offers dairy cattle breeders opportunity for constructive breeding such as is not enjoyed at the present time by any other group of livestock breeders. With careful planning, artificial insemination can be used as a means of developing superior families within the existing breeds so that a constructive program of crossbreeding can be maintained. Thus both the commercial industry and the purebred industry will benefit, although the purebred industry will find itself greatly modified from its present condition. It is, however, highly imperative that plans for such an objective be

initiated at an early date. The reasons for the last statement follow: Cattle breeding moves slowly. Artificial insemination is spreading rapidly and decreases the number of bulls required. Artificial insemination associations have been depending largely on the purchase of proved sires from the outside. Artificial insemination is, therefore, on the one hand, creating an increased demand for proved bulls and, on the other hand, having a depressing effect on the production of registered stock from which proved sires are produced. Through carefully planned programs the associations could be both breeding and proving replacement sires.

Inbreeding. Inbreeding is a sound method of improving the leading registered herds. Inbreeding is a tool with which the skilled breeder can sort the better genetic material from the inferior. There are various methods of proceeding with the development of inbred lines, and there are varying degrees of inbreeding. It is not known which is the best method of inbreeding; it may differ from problem to problem. The optimum level of inbreeding too may vary with different genetic materials. The author has used the following methods successfully in swine and sheep breeding:

1. The foundation stock was selected with the greatest care.
2. The lines started were culled by lines early in the program; the least efficient were dropped.
3. The better lines were culled very severely from within but also expanded as rapidly as possible.
4. The lines were developed by a flexible system of inbreeding. The term flexible is used to indicate that no set program of procedure, such as mating only full brothers to full sisters or the use of only one or two sires in a single herd, was followed in the development of each line. Many full-brother-sister matings were made but some wider matings were also made in the same line. By a flexible system the breeder has the opportunity of speeding up the inbreeding when he has animals on hand that have proved their genetic worth and of slowing it down when he is testing unproved animals. This is more advantageous than following a fixed system; it gives the breeder the opportunity of using the judgment he should have gained through his experiences. In the author's opinion a breeder's success or failure will depend to a

large extent upon his ability to exercise judgment and to follow through to definite objectives.

5. Only the most efficient producers regardless of relationship were saved as breeders and mated. The development of lines that rested on an ancestral foundation of reduced numbers of ancestors resulted. The entire herd at the West Central Experiment Station rests on a foundation of two sows bred at the time of purchase and one boar introduced into these lines. From this slender foundation three lines, since reduced through recombination to one, were developed. This procedure is typical of the development of all the Poland China lines.

The Second Cycle of Inbreeding. When the coefficients of inbreeding reached about 30 per cent in the Poland China lines they were crossed in various combinations and the inbreeding began anew; one line known as the C line is in the third cycle of inbreeding. It is clear that inbreeding in the second and third cycles can proceed much more rapidly than in the first and with a much higher degree of certainty, because the original inbreeding, if conducted successfully, should have weeded out many of the less desirable genes.

The new lines developed from the crossing of two or more original lines were superior to each of the parental lines. The probable explanation is that each of the lines contributed some genes to the benefit of the new line.

The pattern by which the Minnesota A and C lines were developed from several inbred Poland China lines is portrayed by Fig. 97 for the C line. This line arose from seven inbred lines. It is a line that has been put through three cycles of inbreeding, each cycle being followed by a cross and the cross by subsequent inbreeding.

The principle involved in the above procedure is the attempt to give segregation increased opportunity to operate and, through careful performance testing, to select the animals with which to build the line. This line is spoken of as a synthetic line since an attempt was made to compound the different lines into one line (the term synthetic line is used somewhat differently here than by some plant breeders; what has sometimes been called a synthetic line would be better labeled a composite, or pooled, line).

Two valuable lines within the Poland China breed were developed by this process. Each line came to possess a high degree

of uniformity, and, in the investigator's opinion, each is an improvement over the parental stock. In none of the lines, however, was it possible to make marked progress in correcting major deficiencies in the parental stock and breed. These deficiencies can be corrected to a large degree only by making a wide outcross and inbreeding from that point (see gamete selection, page 383).

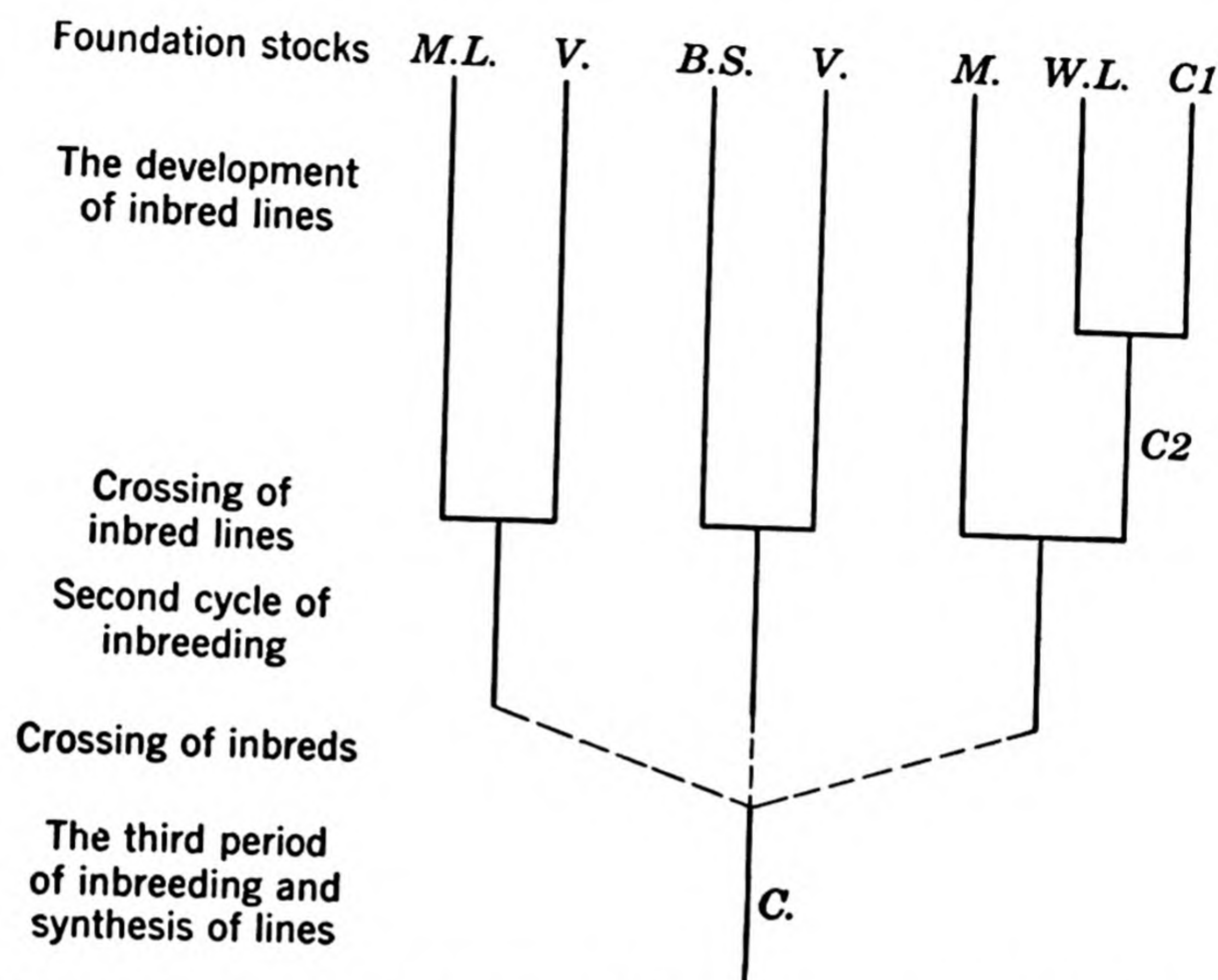


FIG. 97. The development of the C line, a synthetic line.

NEW LINES FROM CROSSBRED FOUNDATIONS

The Minnesota No. 1 Line. The Minnesota No. 1 line was developed from a crossbred foundation. The first cross was produced in 1937 from the use of a Landrace boar on six Tamworth females. A second Landrace boar, two Landrace gilts, and two new Tamworth gilts were added to the herd in 1937. The breeding program for 1938 farrow was as follows:

- 13 F_1 gilts bred to 3 F_1 boars for F_2 litters
- 5 Tamworth females bred to F_1 boars for back-cross litters
- 4 Landrace females bred to F_1 boars for back-cross litters
- 2 Tamworth females bred to the new Landrace boar for F_1 litters

After the above crop of pigs was weaned all purebred stock was disposed of and no new breeding was introduced. Selections were made on the basis of the records made in performance tests. No attention was given to type of ear or other fancy points, although selection was gradually directed to red color. Attention was given to conformation, such as light jowl and shoulder, quality, length of side, and shape of ham; these points of conformation are regarded by the author as part of a satisfactory performance.

During the first years that the herd was bred from within, the selection for a definite type and color could have been speeded up. The reason for holding the process at a slower pace was to try to pick up as many desirable genes as possible from the types that would eventually be discarded. Anderson (1939) has pointed out clearly the desirability of not proceeding at maximum speed in purification, because such a small percentage of the possible genetic combinations are produced in most F_2 or F_3 populations. He pointed out clearly also the advantages of attempting to pick up all possible desirable genes from the parental types even though the type sought is quite different from either parental type.

Anderson's scientific deductions are in accord with the author's experience in swine breeding. It is the author's observation and opinion that in the development of inbred lines from either purebred foundations or crossbred foundations it is good procedure to slow down the progress of inbreeding markedly when the coefficient of inbreeding reaches 15 to 25 per cent. It is his opinion that, in general, the most effective segregation occurs at about this point in the inbreeding program. The general inclination is to wish to speed up and pass through this period of segregation as rapidly as possible. This is the point in the program at which the herd looks least attractive to visitors; at this point the stock is likely to be more criticized than at most other points in the program. The tendency in livestock breeding circles is to be especially critical of lack of uniformity in a herd. On the other hand, this is the point in the breeding program at which the breeder has the opportunity of making the maximum use offered him through segregation. Therefore, he will do well to prolong the period of segregation but take advantage of segregation by

identifying and retaining the individuals that possess the new combination of characteristics desired in the new inbred line.

Selection on the basis of performance within a closed herd automatically has the effect of reducing the ancestry. Fourteen animals were used to establish the foundation, but the number

TABLE LIV. RELATIONSHIP (PERCENTAGE OF BLOOD) OF MINNESOTA No. 1 HOGS TO FOUNDATION ANIMALS

	Animals	Relationship, Per Cent
18-2	First Landrace boar used	44
12-79	Tamworth female from University of Saskatchewan	19
1 of 36	Tamworth female from Iowa State College	23
9 of 36	Tamworth female from Iowa State College	3
13-16	Landrace female used in back cross	6
T 74 R	Tamworth female from University of Alberta, used in back cross	5

that contributed genes to the No. 1 line was automatically reduced to six (Table LIV).

Here, as in the Poland China lines, the number of ancestors becomes reduced materially and rapidly from the number pos-



FIG. 98. Minnesota No. 1 boars.

sible when the system of breeding is within a closed population and selections are made on the basis of performance. Another point of interest and importance is that, by this method of breed-

ing, type, including the little details, becomes fixed automatically. If, however, the breeder has some special desires regarding type of ear, snout, and the like, it is necessary for him to make a special effort to that end.

The Minnesota No. 2. The Minnesota No. 2 line was started five years after the Minnesota No. 1. It rests on a cross of a Yorkshire boar and thirteen females belonging to two inbred



FIG. 99. Minnesota No. 2 boar.

Poland China lines. A straight F_2 population was produced the following year but in the third year a back cross to the Poland China foundation was made for one-half of the litters produced because neither the F_1 nor the F_2 possessed quite so much capacity for growth as was thought desirable.

The No. 2 line was started for several reasons:

1. To attempt to repeat the results being obtained in the development of the No. 1 line.

2. The Poland China lines used in the cross were very good in rate of gain and economy of gain, but weak in fertility and milk production. An attempt was therefore made to combine the rate and economy of gains of the inbred Poland China swine with the fertility and nursing abilities of the Yorkshire. The

quality of carcass produced by the inbred Poland China line was satisfactory but it was hoped that a still better carcass would result. In this instance the task undertaken was somewhat more difficult than in the development of the No. 1 line, for then the two parental breeds had more in common.

3. More genetic diversity was needed in the entire Minnesota swine-breeding project to accomplish most in the ultimate crossing of the lines.

By coincidence, the reduction in ancestors in this line also brought the actual number to six foundation animals, the same as for the Minnesota No. 1 line. The performance of the line is also about the same as that of the Minnesota No. 1, although they are raised at different stations.

The Minnesota No. 1 and No. 2 lines are fulfilling theoretical expectations in that they are crossing exceptionally well. The hogs so produced gain rapidly, make the gains on a low feed intake, and yield superior carcasses with a high percentage of lean.

The U.S.D.A. Development of New Breeds of Swine. In 1934, the U. S. Department of Agriculture in cooperation with the Iowa Agricultural Experiment Station imported 23 Landrace hogs from Denmark. A few Yorkshire hogs were also imported from Denmark, and later Large Black swine were imported from England. These imported strains were crossed with standard breeds in this country in various combinations. A number of back crosses followed and this was followed by inbreeding. All the work was accompanied by rigorous selection on the basis of carefully conducted trials for performance. The work was conducted under the direction of Mr. John Zeller. Seven very promising new inbred lines or breeds have been developed. A brief description of each of the lines and their theoretical percentage of ancestry follows:

Montana No. 1 (Landrace-Hampshire) were developed from a cross of Landrace and unbelted Hampshire. The theoretical percentage of breeding is 60 per cent Landrace and 40 per cent Hampshire. The strain is jet black which is transmitted with a remarkable degree of prepotency. The pigs are long bodied, close to the ground and unusually trim. The line has been released to private individuals and is proving very popular for crossing pur-

poses. This line was developed at the U. S. Range Livestock Experiment Station at Miles City, Montana, in cooperation with Montana Agricultural Experiment Station at Bozeman.



FIG. 100. Montana No. 1 females.

Beltsville No. 1 (Landrace-Poland China) is a line that carries 75 per cent Landrace breeding and 25 per cent Poland China. They are spotted black and white, they have long bodies and

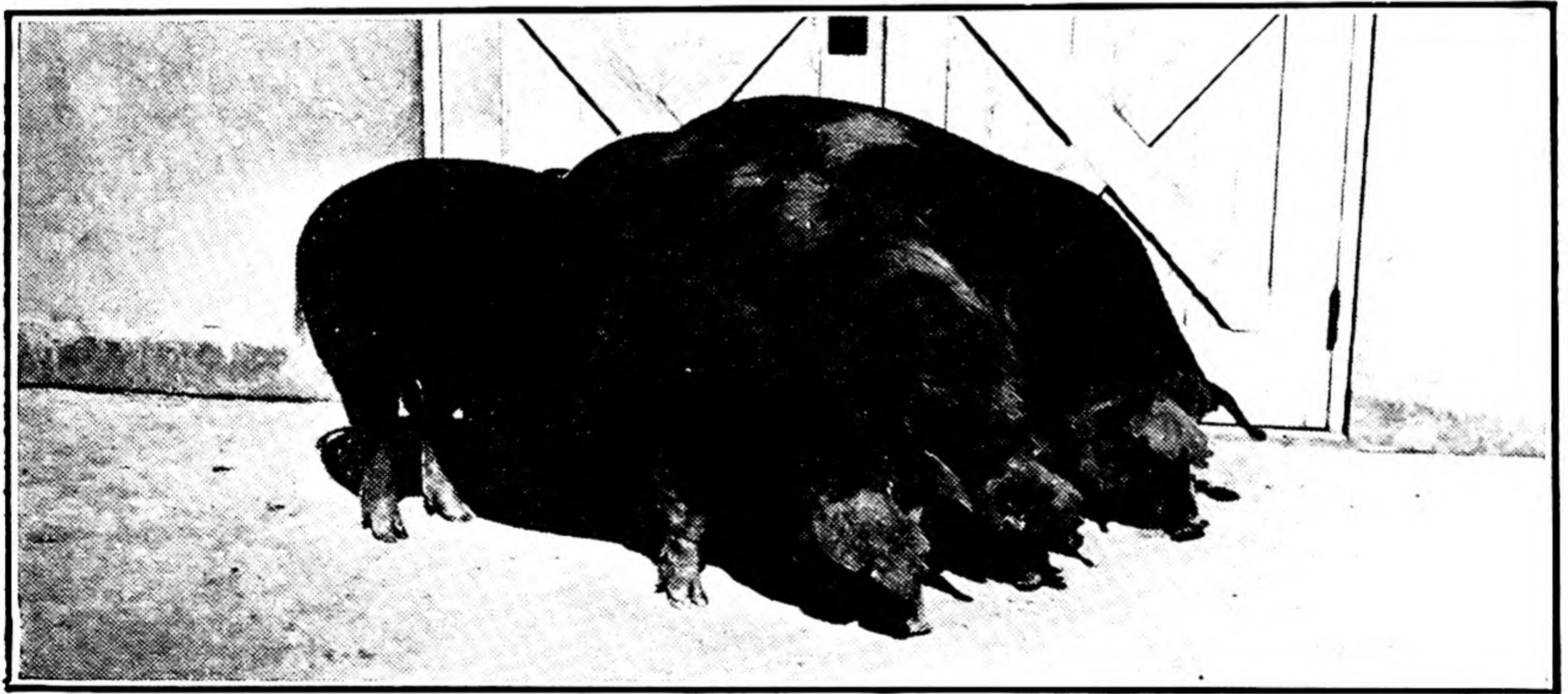


FIG. 101. Beltsville No. 1.

short legs. This line has also been released and is finding considerable favor for crossing purposes.

Maryland No. 1 (Landrace-Berkshire) is theoretically 63 per cent Landrace and 37 per cent Berkshire. The color is spotted

black and white. They were developed at Blakeford Farms, Queenstown, Maryland, in cooperation with the Maryland Agri-



FIG. 102. Maryland No. 1.

cultural Experiment Station. These hogs are long bodied, very trim, and look very promising for crossing purposes.

Beltsville No. 2 (*Danish Yorkshire-Duroc-Landrace-unbelted Hampshire*) is a light-red-colored line that carries a relationship

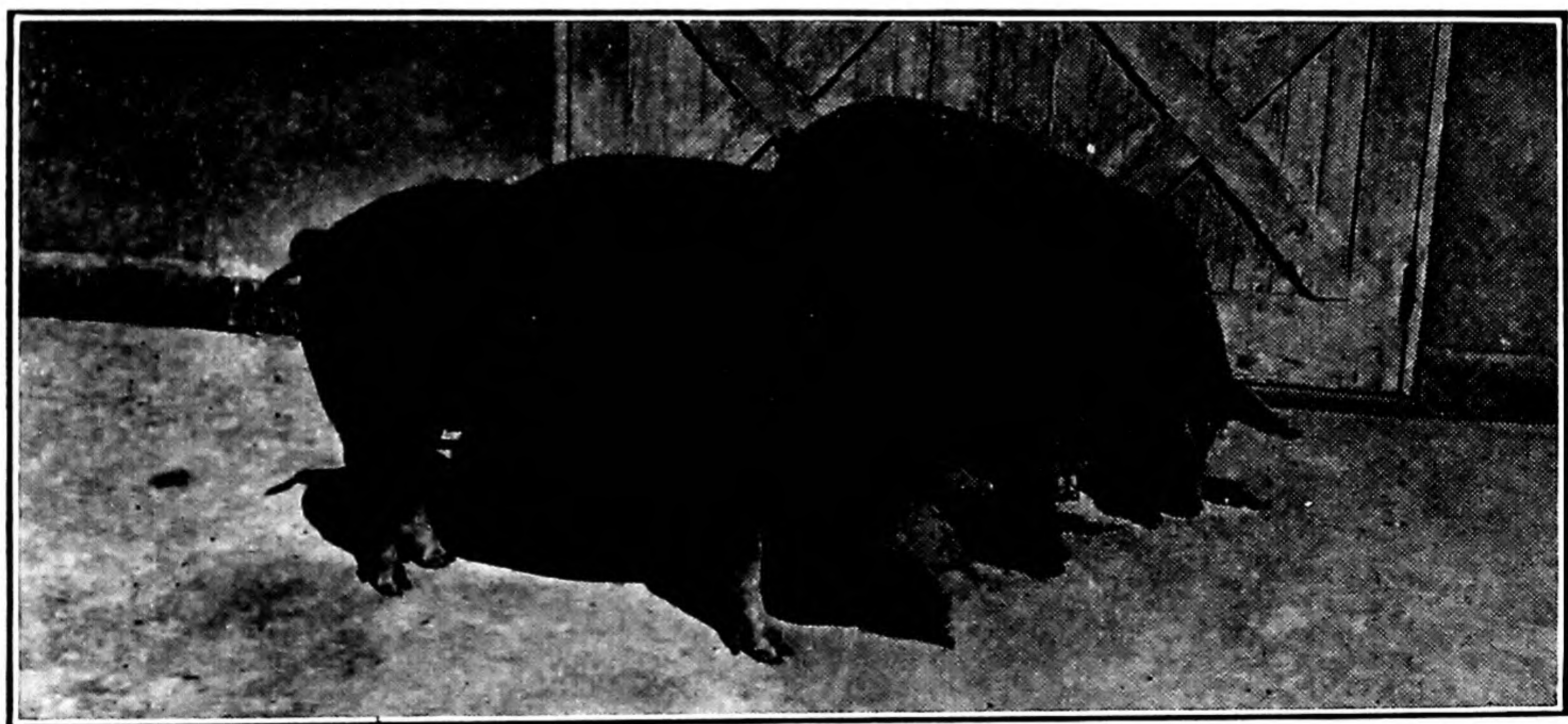


FIG. 103. Beltsville No. 2.

to the parental breeds of 60 per cent Danish Yorkshire, 33 per cent Duroc, 3 per cent Landrace, and 3 per cent unbelted Hamp-

shire. They are an unusually trim and high-quality type of swine.

Landrace-Duroc-unbelted Hampshire carries a theoretical relationship to its parental breeds of 77 per cent Landrace, 15 per

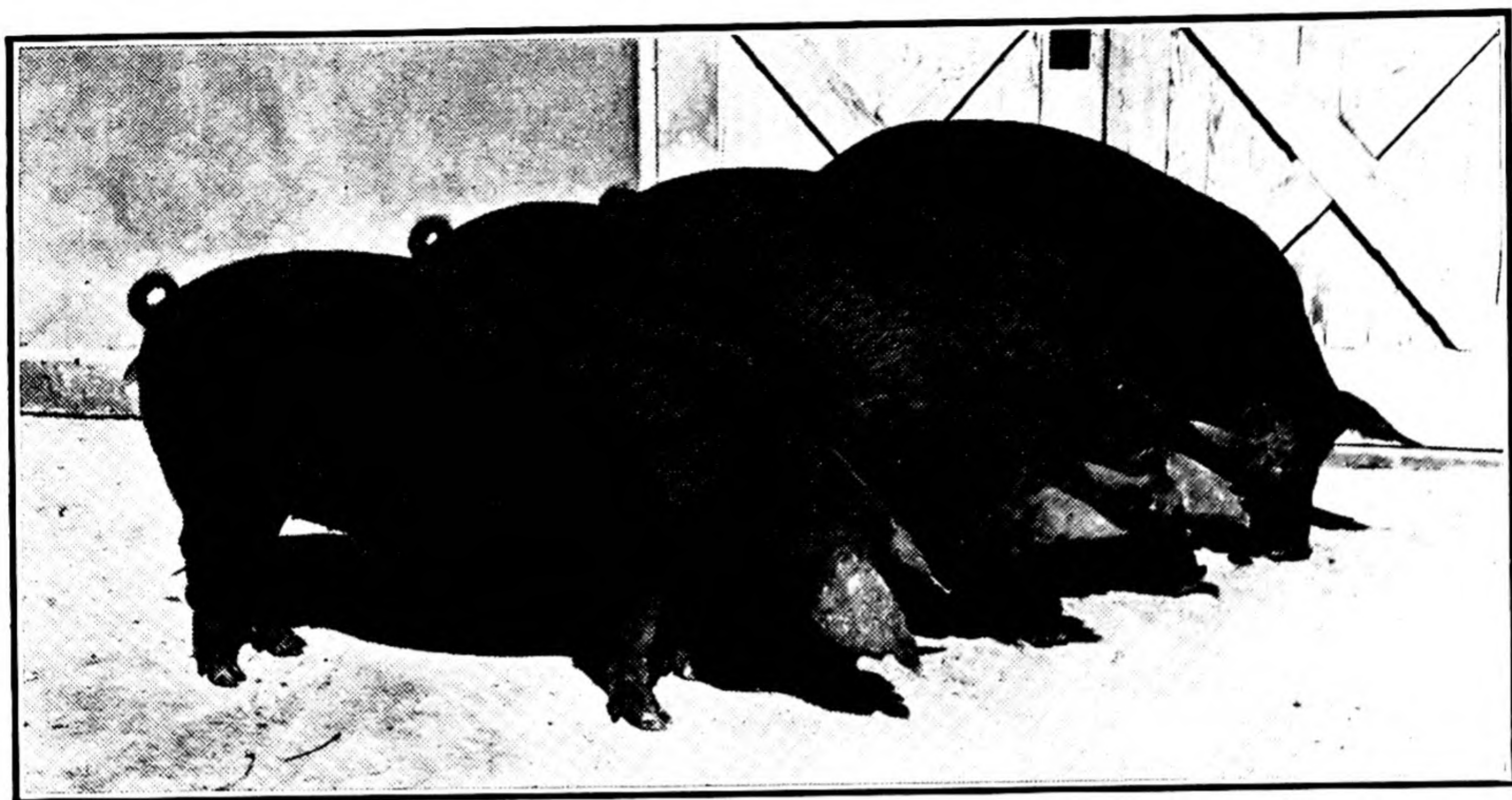


FIG. 104. Landrace-Duroc-Hampshire.

cent Duroc, and 8 per cent unbelted Hampshire. They are red in color and like the others are long bodied and remarkably trim.

Landrace-Large Black is a black strain carrying 75 per cent Landrace breeding and 25 per cent large black.

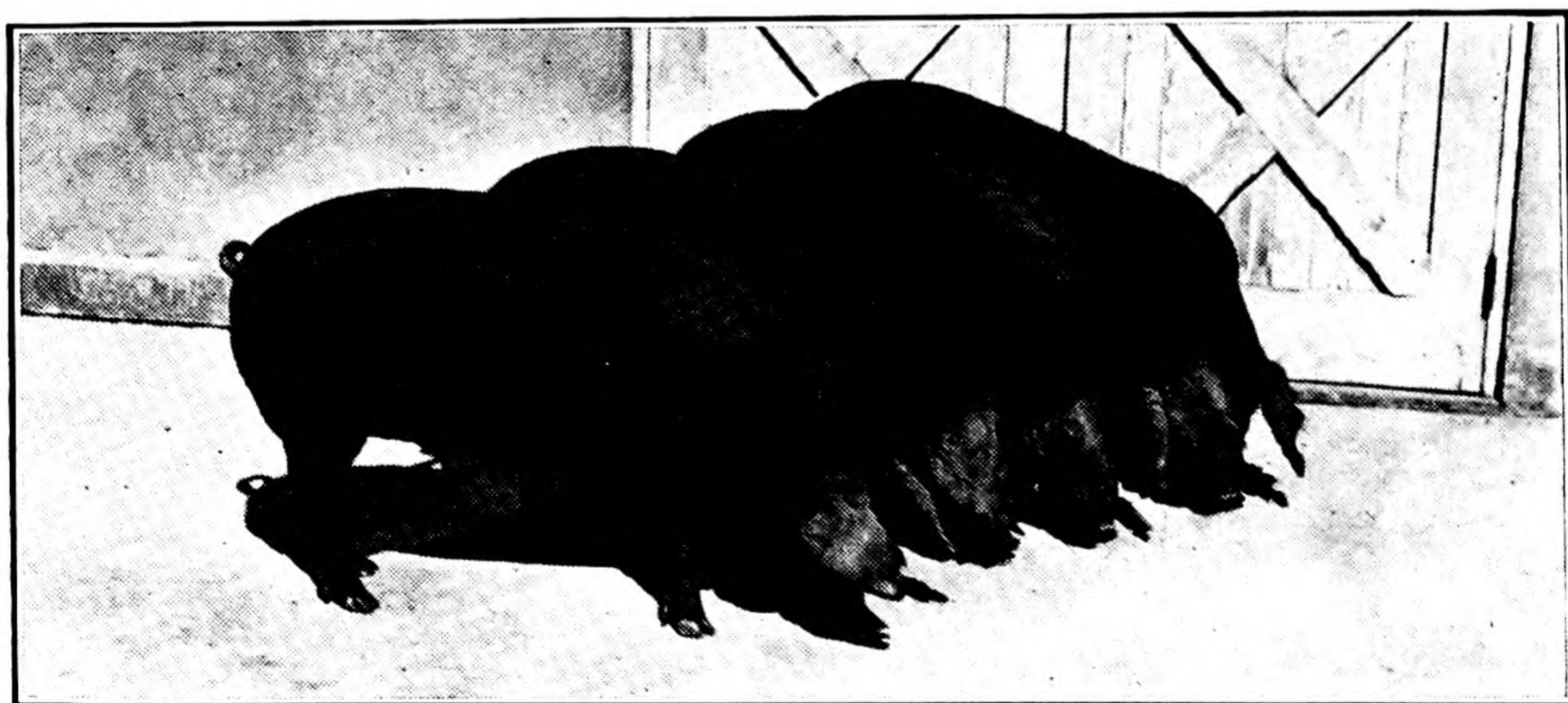


FIG. 105. Landrace-Large Black.

Landrace-Duroc is a red strain carrying a relationship of 75 per cent to the Landrace and 25 per cent to the Duroc parental breeds.

The actual method of procedure in developing all the above lines, with the exception of the Montana No. 1, differed from the development of the Minnesota No. 1 lines in that the original cross was followed by a series of back crosses in an attempt to find the optimum levels of relationships to the parental stocks. In the lines developed at Minnesota, a greater confidence was placed in the opportunity offered by genetic segregation. A back cross to the Poland China was, however, introduced in the Min-

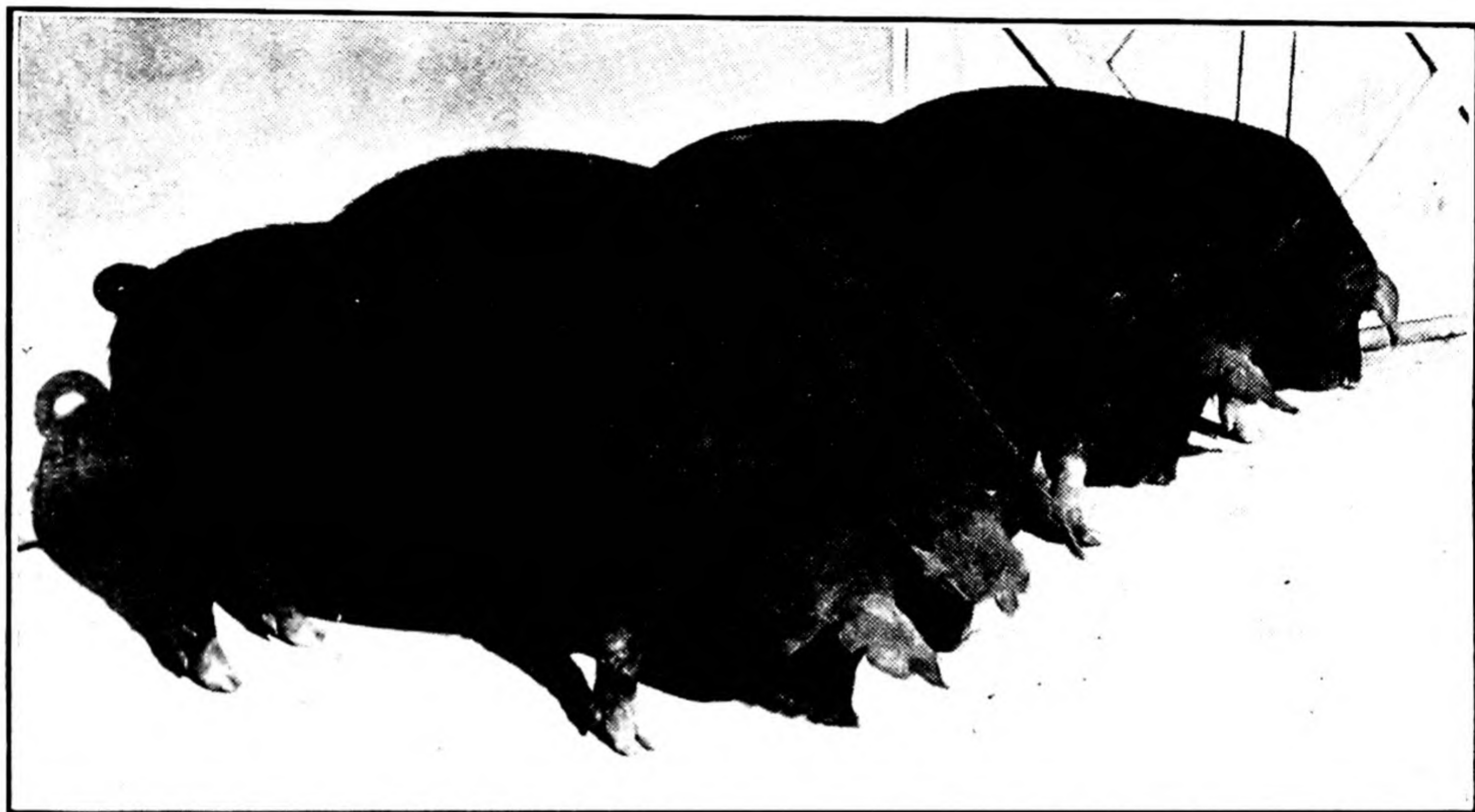


FIG. 106. Landrace-Duroc.

nesota No. 2 in order to speed up some of the correction deemed necessary for an improvement of the foundation.

The basic features, however, by which the new breeds or lines were developed at the Minnesota Agricultural Experiment Station and by the U. S. Department of Agriculture are essentially the same. In both cases, the parental stock consisted of cross-bred foundations. Performance testing was followed as a means of identifying the best segregating types within each crop produced. The best-performing individuals and, in many cases, the sires and dams of the best-performing individuals were retained for the further development of the line. In each case the line was closed eventually to outside breeding; hence inbreeding was used which induced still further segregation.

Not All New Breeds Produced by Experiment Stations. Most of the older breeds of livestock, and many of the more re-

cently developed breeds, were, or are being, developed by private enterprise. The general methods of their individual developments have been very similar. They have been the crossing of different strains or breeds, breeding from within, and selection of the desirable segregates. In most cases, both the objectives and the methods of procedure have been vague. In very few cases, if any, does it appear that the breeders planned to capitalize on segregation and recombination. This is quite clear where considerable effort was directed to finding the optimum percentage relationships to the respective parental breeds. No method is known to determine the true biological relationship of a new breed or strain to each of its parental breeds after segregation and selection have been under way. It is also worth noting that back crossing in an attempt to fix the assumed optimum levels of relationship retards segregation with the accompanying recombinations rather than inducing and capitalizing on it.

Several of the more recently developed breeds were mentioned in Chapter XIV, and several of the new breeds or lines of swine are discussed in this chapter. In a book of this type, there is no occasion to mention each new breed or discuss their respective merits, as the emphasis here is on methodology. Two developments of the twentieth century are of interest in this connection. One of these is the development of the Broadbreasted Turkey, on the one hand, and the development of the Beltsville White, on the other. The differences in weight between the two types is very marked.

The other development referred to above is the widespread interest on the part of the commercial cattlemen of Texas and the Southwest in larger beef cattle than the type favored in the American show ring. The Zebu and Charlette cattle have found considerable favor as sources for useful genes not found in the British breeds of beef cattle. The Beefmaster cattle of the Lasater Ranch, Falfurrias, Texas, and Mathesen, Colorado, are a product of this move, and an illustration of a commercial firm mixing the genes and then relying on segregation and the selection of new combinations to achieve desired ends.

In 1908 Mr. Edward C. Lasater began using Brahman sires on Hereford and Shorthorn females. The Gir Brahman, Nellore, and Guzerat strains of Zebu were all used. The stock was eventually interbred, and emphasis in selection was placed on the

following characteristics: (1) disposition, (2) fertility, (3) weight, (4) conformation, (5) thriftiness, and (6) milk produc-

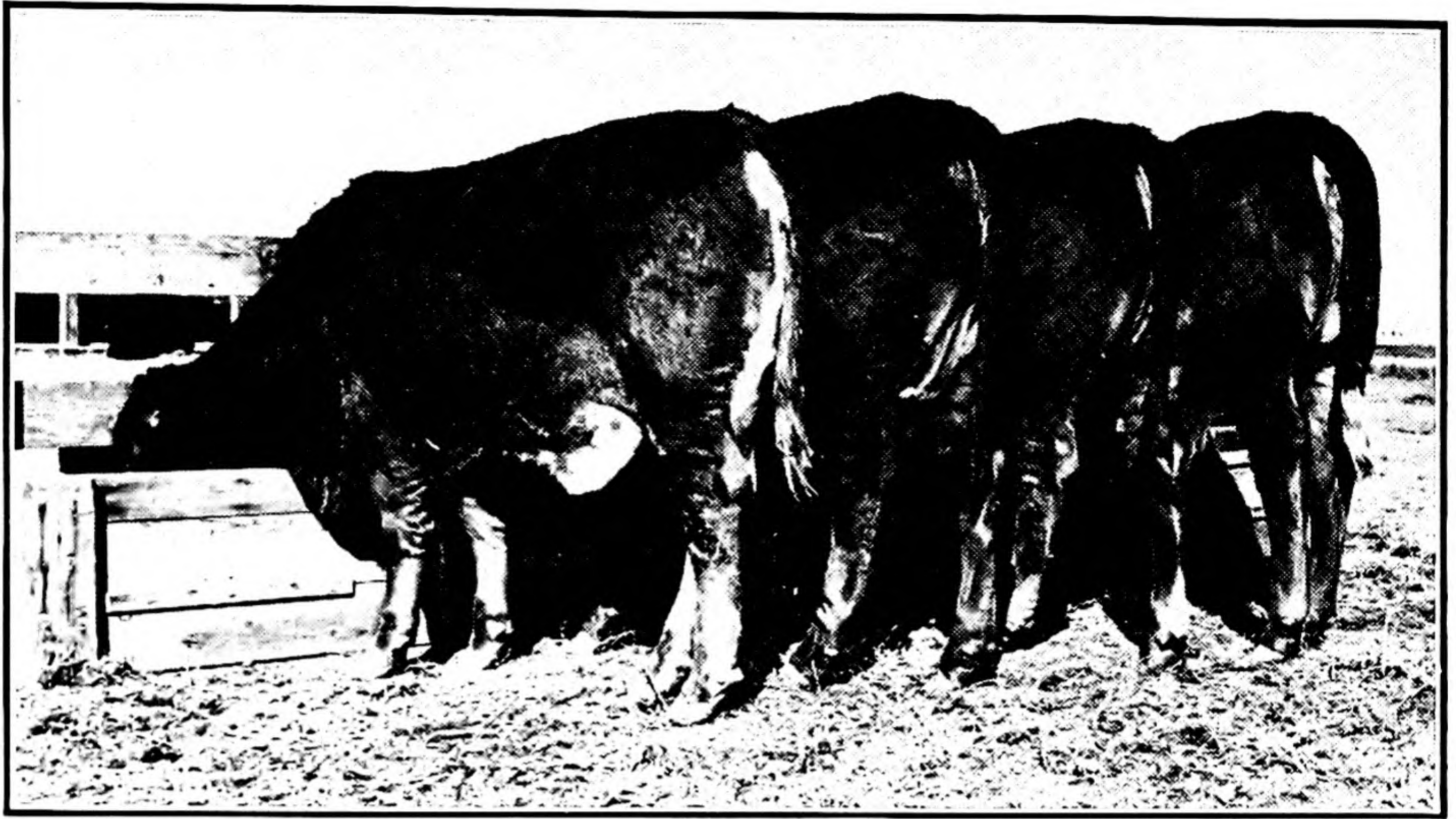


FIG. 107. Yearling Beefmaster heifers. (Courtesy of Tom Lasater.)

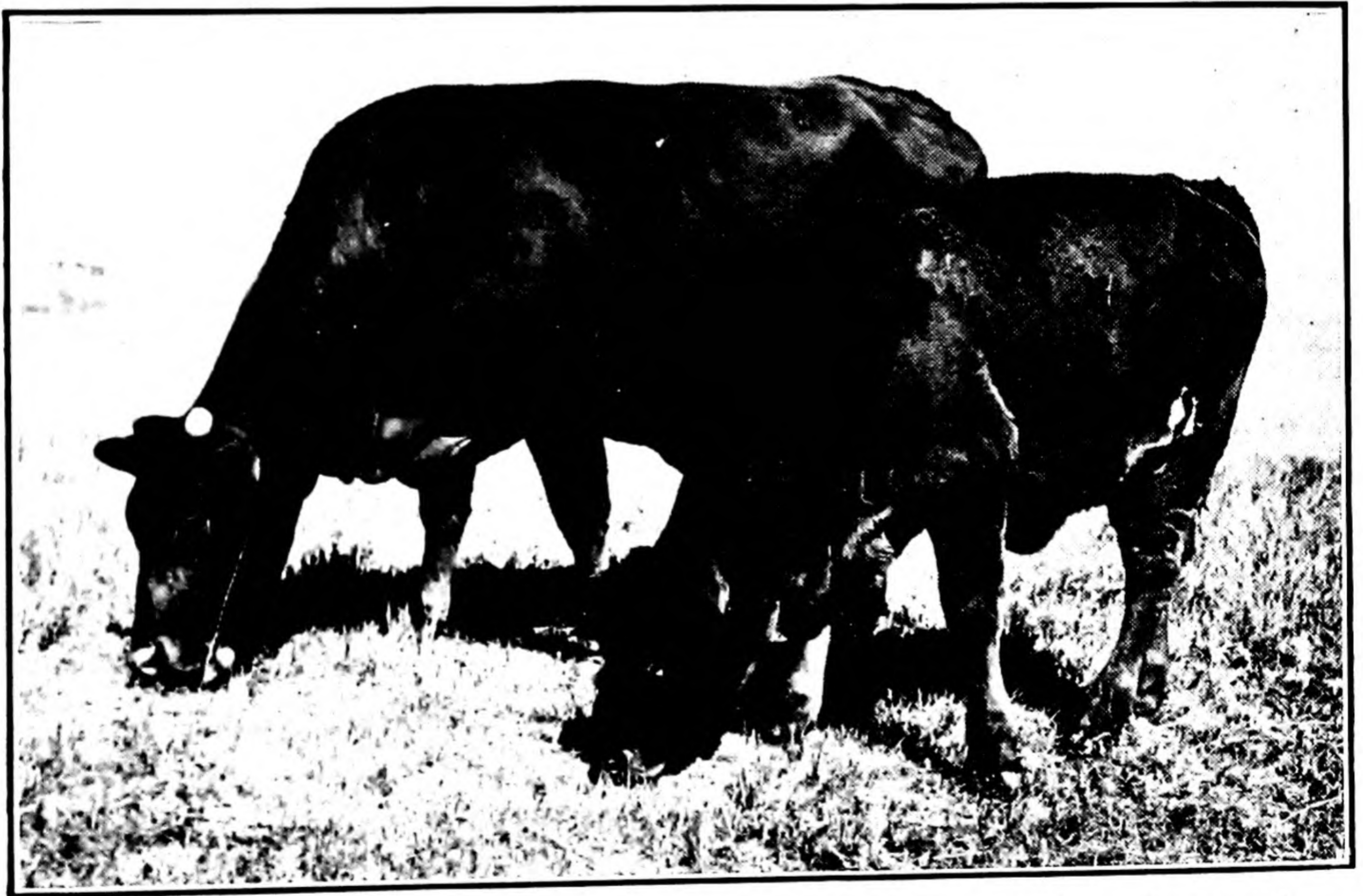


FIG. 108. A Beefmaster cow and calf. (Courtesy of Tom Lasater.)

tion. These same characteristics had previously been emphasized in the development of the strains introduced into the Beefmaster Foundation. Samples of the product are illustrated in Figs. 107 and 108.

The Principle of Recombination. That there is no known method of making better genes cannot be overemphasized. (Mutations have been produced artificially in plants and *Drosophila*.) The breeder has the opportunity of improving his stock by sorting the better genes from the poorer ones, by introducing new and superior genes to his gene collection, and by regrouping the gene combinations. The first of these three methods has received by far the major attention in animal breeding. The second has been used extensively but not emphasized greatly. Nearly all, perhaps all, our breeds rest on crossbred foundations of one kind or another, but this is generally de-emphasized. The third, the recombination of genes, has received practically no emphasis in animal breeding circles. It is closely related to the second; in fact new genes must be introduced in order to give full opportunity for a regrouping of the genes.

In the author's opinion the regrouping of the genes offers the constructive animal breeder his greatest opportunity for improvement. It offers him also the greatest opportunity for retrogression. The total possible number of new gene combinations is beyond calculation because there is no way of knowing how many crossovers may occur or the size of the various allelomorphic series. Even if crossovers or allelomorphic series are not taken into consideration, the possibilities for reorganization are almost beyond the imagination. The pig is credited with 19 pairs of chromosomes; if then we are dealing with only 1 pair of gene differences for each pair of chromosomes, there is the possibility of producing 524,288 different kinds of gametes, and 1,162,261,467 different genotypes. Because there are many genes on each chromosome, allelomorphic series, crossovers, and gene interaction, the possibilities for finding better gene combinations become practically unlimited. The probability that the best gene combination has been found or will be found in the near future is remote.

A striking illustration of the possibilities in constructive breeding through the principle of recombination is to be found in contrasting the results of two different objectives in the University of Minnesota swine-breeding research. One project has as its objective the breeding of swine that will reach market weight in a minimum of time and yet produce a high-quality product at a minimum of expense. The other project, a Hormel Institute-

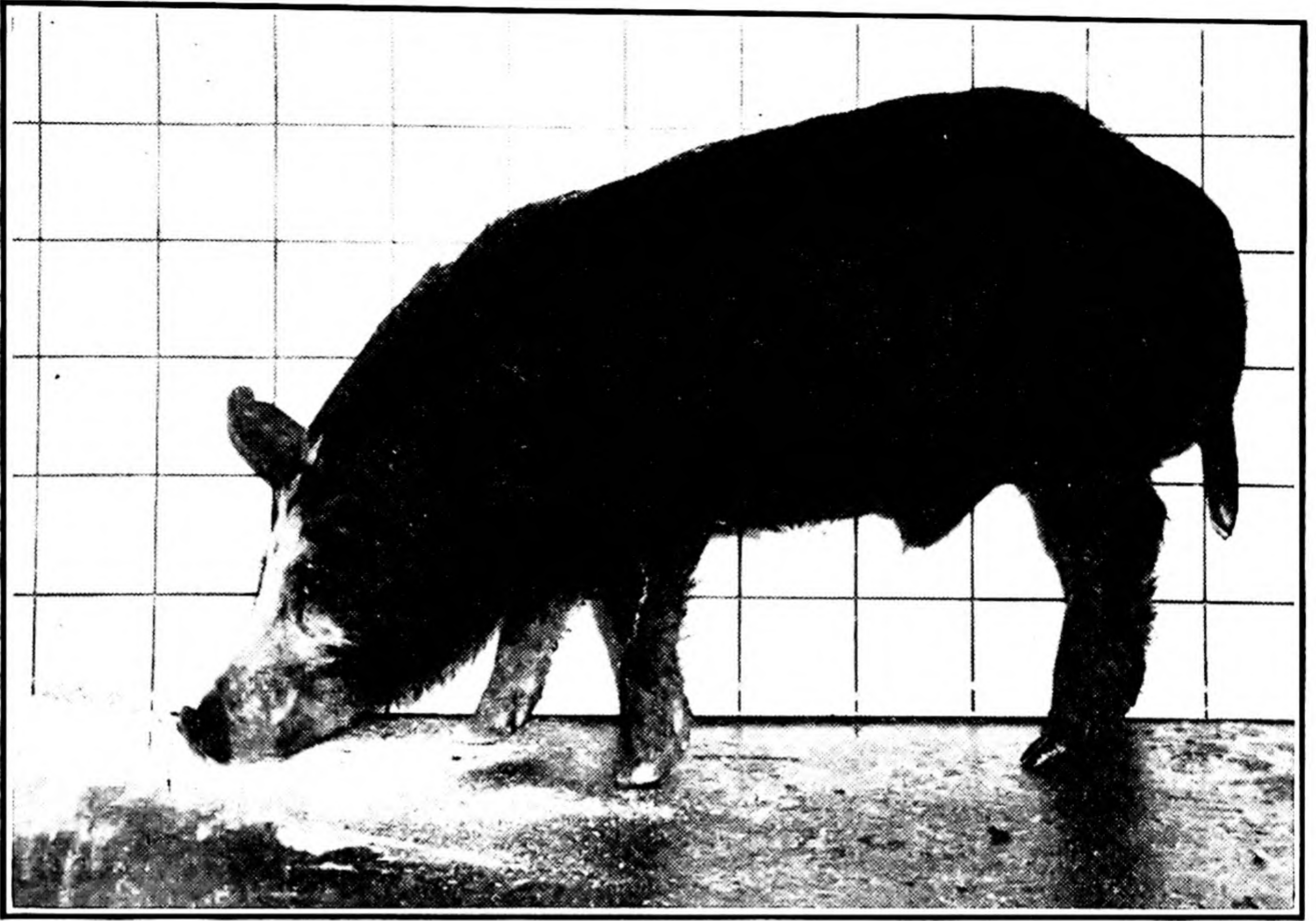


FIG. 109. A miniature pig, weight 76 pounds, at 238 days. Contrast with Fig. 110.



FIG. 110. A litter of Minnesota 1-3 crossbred swine, litter weight 3032 pounds at 140 days. Contrast with Fig. 109.

University of Minnesota project, has as its objective the development of a miniature pig to furnish a low-cost, easily maintained pig for medical research. The foundation stock for the latter was drawn from three different sources, all of which were small-sized swine, but not as small as the early segregates, several of which weigh 40 pounds or less at 154 days. Figure 109 illustrates one of the miniature pigs that weighed 12 pounds at 56 days, 40 pounds at 154 days, and 76 pounds at 238 days. In contrast, Fig. 110 is a litter of Minnesota 1-3 incross swine, 15 in number, that at 140 days weighed 3,032 pounds, an average of 202 pounds.

The very vastness of the possibilities for improvement through recombination offers equal opportunity for regression or for the breeder to become lost in the process. If, however, the breeder keeps a few definite simple fundamentals in mind there is little excuse for becoming lost. They are:

1. Have some definite objective, or objectives, in mind.
2. Introduce outside genes for a definite purpose.
3. Draw the outside genes from a source that the breeder has reason to believe will supply what is wanted.
4. Use inbreeding as the seed producer uses the fanning mill to separate the chaff, the weeds, the damaged seeds, the light seed, and the foreign materials from the sound seed.
5. Set up a testing program designed to reveal as accurately as possible in which of the above classifications each animal belongs.
6. Be prepared to cull heavily and early both individuals and lines.

The Testing Program. Records for performance testing are discussed earlier in this chapter, but the environmental conditions under which the records are gathered are of equal importance. The race track provided an ideal proving ground for the race horse; the desert provided an equally ideal environment for the development of the Arabian horse, an animal with remarkable stamina.

If animals that possess maximum ability to forage for themselves over the open range are wanted, the open range is the ideal proving ground for the development of such a line; the deeply bedded box stall is scarcely the appropriate environment. On the other hand, under many conditions there is more profit in

rearing livestock under more favorable environments than the open range. In general, the most profitable swine, poultry, and dairy production takes place under a favorable environment, approximating pampered conditions. Here the type of animal wanted is one that will respond readily to this kind of environment.

A line developed under either of the above conditions is not likely to prove adaptable to the other environment; therefore, the breeder should decide at the outset what his objective is. Merely to set out to breed better animals is far too vague an objective. Having a definite objective in mind, the breeder needs to devise a proving ground suited to that objective.

PROPOSED BUT NOT FULLY TESTED METHODS FOR THE DEVELOPMENT AND IMPROVEMENT OF LINES

A Simplified Procedure for Developing Inbred Lines. In a research program it is usually necessary to study many details in procedure and records that become impractical when the principles developed from the research are put into practice. The author has, therefore, been working on plans for a simplified and more economical method of developing inbred lines. To date, the system has been used only in sheep breeding and in one poultry-breeding project where the author has served as a consultant. The scheme embodies pedigreeing from the female side only. Females are, therefore, lot-bred, a group of females being turned with two or more carefully selected males.

The advantage of the system appears to be considerable simplification in procedure and time involved in contrast to making individual matings. In addition, there appears to be an advantage in getting a higher degree of fertility than is obtained when one male is used in lot breeding.

A disadvantage of the system is, of course, that a detailed record with regard to the sire used is not available. Exact estimates of the coefficient of inbreeding can never be obtained, nor can a complete pedigree be written of the stock produced. From a genetic standpoint neither of these criticisms is particularly important. The important job in livestock breeding is to produce superior stock with a high degree of regularity. An objective

in the development of inbred lines is to develop inbred lines that are of optimum value and to do this with a minimum of expense. If the breeder's system of selection is as successful as it should be, and he naturally is striving for that, then he should select a greater proportion of the offspring from the more or most useful sires used. Hence, the genetic results should be the same, regardless of whether the progeny can or cannot be pedigreed in relation to their sire. The simplified method does, however, pre-



FIG. 111. Minnesota No. 100 sheep, a breed "in the making," resting on a foundation of Rambouillet, Border Leicester, and Cheviot. Another illustration of working for a resorting of the genes and a test of recording ancestry from the female side only. (Courtesy of Walter Hunt.)

vent the continued use of the proved sire, but, if the program of selection is such that his sons and daughters are retained, the net results should be the same.

A further advantage of this system of breeding appears to be that it encourages a more severe culling of the less fit, particularly with respect to fertility. The most serious problem encountered to date in the development of inbred lines has been a lowering of the degree of fertility, due particularly to lack of sex drive on the part of males. The proposed system appears to offer an advantage of tending to emphasize sex drive by automatic selection. The male with the greatest amount of sex drive will be the one that sires most of the offspring. The tendency in hand mating is to encourage the use of slow-breeding males, and, for that matter, slow-breeding females, in order to retain some desirable characteristic possessed by these less active individuals.

The author has been using this system in the development of three new breeds of sheep, and he is convinced that the method is practicable and at least as effective as matings made under the complete pedigree system. Actually this is a very old method of livestock breeding. The Scotch breeders of Hill sheep have used this method for many years. Moreover, they have used it with a high degree of success. Some of the very best flocks of sheep in the world are to be found in the hands of the Scotch breeders who have followed essentially this system. They, of course, have not selected on as careful a plan of performance testing as should be practiced in a modern breeding program, but under their conditions in which the sheep for the most part feed on the scant forage of the hills a very good proving ground is provided.

The Back Cross. Backcrossing is the mating of F_1 to one of the parental types; this is usually repeated for several generations and followed by inbreeding. The purpose is to attempt the transfer of some desirable characteristic from line *B* to line *A*. It is usually attempted in cases where the breeder has a line strong in most respects but that needs improvement in one characteristic. In that case line *A* is crossed to a line that is especially strong where line *A* is weak. During the backcrossing especial care is given to selection of individuals that possess the trait introduced by *B*.

The back cross method has been used successfully by many plant breeders. Some of the older animal breeders used it to advantage, but for the most part animal breeders have not been especially systematic in its use.

The back cross has been the forerunner of gamete selection, convergent improvement, and recurrent selection. A discussion of these methods follows.

The back cross has also been used in several instances in an attempt to find the best proportion of relationship to retain to the two parental types, *A* and *B*. This necessitates backcrossing several times to both parental types to find the optimum respective relationships to be retained. Under special circumstances, such as the development of the Santa Gertrudis cattle, there is a reason for this method of procedure. In the case of the Santa Gertrudis the attempt was to maintain enough Brahman breeding to give the new stock a protection against heat

and ticks. Serious objections to this type of backcrossing are that it is time consuming and it fails to give segregation the optimum opportunity of working.

Gamete Selection. Stadler (1944) suggested a method of improving inbred lines of corn which he called gamete selection. The method of procedure was:

1. An inbred line of known performance is exposed to gametes from an open-pollinated variety.

2. The seed from the cross are grown.

- a. As many F_1 plants as there are gametes to study are selfed.

- b. Pollen from the selfed plants is used in crosses with tester stock which is compared with crosses of the parental inbred \times tester. The purpose of this is to identify gametes that have improved the inbred line.

3. Seed from the plants which cross to best advantage are then used as the basis for further breeding and selection.

The basic principle involved by the proposed method is to expose a fixed inbred line to mixed pollen from an open-pollinated variety. By careful observation, the most desirable crosses were marked and the seed saved for further testing. A gamete or several gametes that complemented the inbred line to advantage were thereby picked up from the open-pollinated stock and eventually incorporated in the line.

The method proposed by Stadler is one that has been used *in substance* for many generations by constructive livestock breeders. It is well known that Lovejoy used this method very effectively in the breeding of outstanding Berkshire swine some years hence. Lovejoy is credited with never introducing a complete outcross in his herd; he usually preferred to buy a female or two and mate her or them to his favorite sire and then, if the results were promising, use either a son or grandson of the outcross in the herd. In this way, according to Lovejoy, "new blood" was introduced into the herd gradually.

In travels in Britain the author found that those whom he considered the outstanding breeders of Hill sheep had for generations followed a similar system. They, according to their story, made it a practice never to buy a sire or sires, but occasionally would buy one or several females; then sons or more likely grandsons of these matings would become herd sires. The author

found the same basic principle being used by the outstanding Aberdeen-Angus breeders of Scotland.

It is true that the technic of procedure is slightly different in the above illustrations with animals from Stadler's technic with corn. The basic principle, however, is the same, namely, the search for a gamete or several gametes that will complement the genetic structure of the herd, flock, or line. Technics must, from necessity, vary from species to species, dependent upon both biological and economic factors.

Gametic selection is essentially a "dressed up" old method of breeding. Nevertheless, it has been a very successful method of improving livestock and of maintaining a herd in a high state of genetic perfection and in a rather stable manner. During recent years, the method has received very scant attention from animal breeders. It is a method that offers the opportunity of holding what the breeder has and yet reaching out in an attempt to improve that line without seriously endangering what he has already built in the line. Animal breeders will do well to revive interest in this method; that applies to both the breeders in the field who are breeding outstanding herds of pedigreed stock and to the experimental breeders who are developing and attempting to improve existing inbred lines.

The Synthesis and Pooling of Lines. Hayes and Garber (1919) suggested the possibility of using what they term synthetic varieties of corn. The term is used as a description of a complex hybrid made up of several inbred lines or single crosses propagated as a variety in isolation and with open pollination. Sprague and Jenkins (1943) also worked on synthetic lines and concluded that (1) synthetic lines yield approximately the same performance as well-adapted open-pollinated varieties, and (2) synthetic lines seem to have their greatest usefulness as temporary substitutes in areas where adapted double crosses are not yet available and also as a reservoir of desirable gene combinations.

Hayes, Rinke, and Tsiang (1944) made a more critical study of the possibilities of so-called synthetic lines. They tested twenty inbred lines in all possible combinations. The eight lines which gave the highest average yield in single-cross combinations with each other and which represented wide genetic diversity were chosen as the basis of a synthetic line. Samples of the

eight inbreds were mixed and planted in an isolated plot in 1941. The synthetic variety was for three years compared with one of their best hybrid corns and with several open-pollinated varieties. The over-all results were that the synthetic variety yielded slightly but not significantly better than the hybrid line, but better than the open-pollinated varieties.

Kinman and Sprague (1945) developed a formula for determining the most efficient number of lines to be used in a synthetic variety. They came to the conclusion that four to six lines appeared to be the most efficient number.

A major objective of the plant breeders as described above is the maintenance of a hybrid state in a variety over an indefinite period of time. The term *pooled* would better describe the procedure outlined. A synthetic line is better illustrated by the process by which the Minnesota C line of swine was developed. In this case, the crossing of the two or more inbred lines is followed by sufficient inbreeding to raise the level of homozygosity to the level possessed by the lines put into the new variety. The development of a new breed from a crossbred foundation of two or more other breeds is a process of synthesis rather than a pooling of the breeds or lines. The two methods have some similarities but differ in objectives and in procedure.

The Application of Synthetic and Pooled Lines in Animal Breeding. If we assume, and there is sufficient reason to do so, that the development of new breeds from two or more old stocks or breeds is accompanied by some genetic purification, then the process by which the breeds were built is one of synthesis. It, therefore, is an old method of animal breeding. The combining of two or more inbred lines into one new inbred line that is as highly purified as the average of the foundation lines is a new method of utilizing synthesis in animal breeding. It has already been used sufficiently to recommend its further utilization.

The pooling of several lines has never been tested in livestock. A rather large number of inbred lines are in the process of development—so many that their maintenance as distinct lines may prove costly. On the other hand, dropping them completely may result in the loss of valuable genes. A pooling of several lines that rest on somewhat common backgrounds may in some cases provide a solution to the problem.

Convergent Improvement. Convergent improvement was first proposed by Richey (1927) as an aid in distinguishing between two theories of the cause of hybrid vigor and as a method of improving inbred lines of corn without altering their combining values. Richey and Sprague (1931) reported that inbred parents could be improved by this method. The method in brief is as follows: Two inbred lines, A and B , cross well, but the desire is to improve both of the lines. The lines are crossed to produce an F_1 . The F_1 is backcrossed to each recurrent parent, as $(A-B) \times A$ and $(A-B) \times B$. The resulting offspring are in each case selected very carefully for the characteristics of the non-recurrent parent. As, for instance, the $(A-B) \times A$ progeny are selected for the possession of B characteristics, and, in like manner, the $(A-B) \times B$ progeny are selected for possession of A characteristics. The reason for this is the attempt to incorporate genes from the B line into the A complex of genes and to incorporate genes from A into the B line. The backcrossing is continued for several generations with continued selection for characteristics of the non-recurrent parent. Following backcrossing, the modified lines are inbred for several generations and then tested for combining ability with each other.

Murphy (1942) reported that it was possible to make marked improvement in the lines as regards vigor and other desirable characteristics and that the yields of the recovered lines were significantly higher in crosses than were those between the original parents.

Convergent improvement appeared in the early 1940's as a very promising method for the improvement of inbred lines of corn. It, however, has not been generally accepted as a practical method of improving inbred lines of corn. Other methods appear to be offering corn breeders greater opportunities for constructive work.

The benefits from convergent improvement would appear to be dependent on the accumulation of a greater number of genes having additive effects rather than any major improvement in combining ability between the two lines. It would not be surprising if convergent improvement were to prove of more practical benefit to animal breeders than it appears to have been to corn breeders, because it is so much more important in animal breeding than

in corn breeding that the inbred lines be good performers themselves.

Recurrent Selection. The principle of recurrent selection developed out of convergent improvement. Hull (1945) proposed the principle as a method of developing inbred lines of corn that would cross to better advantage than those developed by past methods.

The principle involved is designed to take greater advantage of the interaction of genes and the resultant overdominance by selecting inbred lines during their developmental process for the purpose of better complementing each other. Although recurrent selection is in some ways an outgrowth of convergent improvement, the success of each depends upon different basic principles in achieving ultimate desirability. The success of convergent improvement is dependent primarily on the ability of the breeder to accumulate a greater number of genes having additive effects, whereas, in recurrent selection, the ultimate success is dependent upon the accumulation of genes in two different parental lines which interact to increased advantage.

The method proposed by Hull consists, essentially, of recurrent selection from a crossbred population for combining ability with a single highly purified line, labeled the tester. The tester seed should come from a line that has been proved for general combining ability. It should be a desirable inbred line which is relatively homozygous.

The seed source or the crossbred population may be from a common variety or from a cross of varieties or a cross of superior inbred lines. It is important that it possess considerable breadth of ancestry and heterozygosity.

The technics of procedure as outlined by Hull are with some modifications the rather standard technics of corn breeding. The basic principle involved is to test individual vigorous plants from the crossbred population in crosses with the tester (purified) line. At the same time, self-fertilization is practiced on the crossbred plants that are used to fertilize inbred plants. After the test of the combining ability of the different plants, the crossbred plants that combined best with the tester stock are saved for further breeding. They are inbred by selfing at the time the plants are crossed individually with the tester stock. This process is continued over a number of generations, the principle being

to pull out of the crossbred stock a combination of genes that combines best with the tester stock.

Comstock *et al.* (1949) suggested an improved method of using recurrent selection, which they named reciprocal recurrent selection. The method proposed was to develop two stocks simultaneously and select both stocks for their ability to combine with each other. The method may be described briefly as follows: Two open-pollinated stocks or two different crossbred populations, labeled *A* and *B*, are to be developed so as to complement each other in crosses. Specific plants from stock *A* are crossed to a number of plants belonging to stock *B*, and, in like manner, a number of plants from *B* are used to pollinate plants from *A*. By this method of procedure it is possible to find plants in each stock which combine unusually well with the other stock. All plants are selfed, and the pollen from the plants is tested in crosses with the other line. The seeds from the selfed plants that have performed best in crosses are saved for breeding. This process is continued for a number of generations. The objective in this procedure is to build up in line *A* and in line *B* gene complexes that complement each other especially well and will, therefore, build each of these stocks so that it will cross unusually well with the other one. Recurrent selection is developed to take advantage of gene interaction or specific combining ability.

For several reasons the application of recurrent selection to animal breeding appears to be much more difficult than its application to corn breeding. One reason is that its advocates generally admit that the over-all effect on the inbred lines themselves will be somewhat deleterious, in contrast to the over-all effect to be expected from convergent improvement, because selection is made on the basis of the ability to combine with another stock rather than to build up desirable gene complexes in the inbred line itself. The latter procedure puts more emphasis on building up additive gene effects for vigor. The lowering of performance in an inbred line of livestock is far more serious economically than it is in corn. It is also far more serious biologically because the animal breeder does not have the degree of fertility to work with that most plant breeders have. He cannot greatly lower the degree of fertility and still maintain his stock, irrespective of the financial problem.

A further complicating factor is that, if any scheme of selection is to be effective, the breeder must have sufficient individuals so that the program of selection will allow him to discard individuals rather freely. Recurrent selection carried out so as to allow the breeder enough individuals to select effectively will require more individuals than most animal breeders have at their disposal. One reason that so many individuals will be required for him to carry out a program of recurrent selection effectively is that the characters that have given animal breeders the greatest amount of trouble during inbreeding have been fertility and survival. In order to test for fertility and the ability of the mother to bring her young to sexual maturity, it will be necessary for the animal breeder to test crosses of the two recurrently selected lines as breeders themselves. In the meantime, he must retain the individual parents of the crossbred stock that needs to be tested as breeders. This procedure will inactivate a sufficiently large number of individuals to make the scheme quite difficult. Since the parental stock must be saved until their crossbred progeny are tested as breeders, the effect is to slow down materially the advance of generations. This also increases the expense of the project.

It is possible that with time and the application of ingenuity some short cuts or abbreviated methods of applying recurrent selection to animal breeding will be developed. Theoretically, the method offers possibilities. There is at this writing some question as to its practicability. Very likely the method will be given a test in the years to come. It is to be hoped that several experiment stations will give the method a comprehensive trial. To give it a thorough trial, large numbers will be required in order to allow for the possibilities of selection for all characteristics. It would be extremely fortunate if at least three experiment stations were to cooperate in a trial of this kind; each station to undertake the development of two inbred lines but each of three stations to undertake the development of two different inbred lines. If all three stations were successful in their programs, the end result should be the development of six very useful lines and lines that might be worked out very successfully in a scheme of rotational crossbreeding using incross males.

At the same time, if three stations were to undertake the experiment independently it should furnish a satisfactory test of

the feasibility of this method of developing inbred lines of livestock for crossing. The problem, however, becomes more complicated as the degree of fertility decreases. It is entirely feasible that, if the method proves workable in corn, it may also be workable in poultry, and yet may not be workable, because of the difficulties mentioned above, in four-footed farm animals. Then again, this plan or another plan may be workable in swine but not in sheep or cattle because of the differences in degrees of fertility.

THE MAINTENANCE OF A LINE OR HERD

After the superiority of a closed herd or line has been established, it becomes of major importance that the herd or line be maintained in the status quo genetically, or at least with no deterioration or marked genetic fluctuations which so often follow outcrosses. Once a superior line has been established, it is important that the stock be maintained in the status quo for a considerable period of time to allow breeders to draw on the herd, and to provide a constant stock for long-time research in fields other than genetics.

The author has been working on this problem since 1947. At that time it was decided to attempt to hold the Minnesota No. 1 foundation herd in the status quo. The plan decided on was to continue intensive selection on the basis of performance but to use about ten boars each year. Table LV gives a summary of the production of the herd five years later. A test of this type

TABLE LV. PERFORMANCE OF THE FOUNDATION HERD OF MINNESOTA NO. 1 SWINE FIFTEEN YEARS AFTER THE HERD WAS CLOSED AND FIVE YEARS AFTER INITIATING THE PLAN OF USING TEN HERD BOARS EACH YEAR

Number of sows	37
Average age of sows	21.4
Average inbreeding of dams	0.37
Average number pigs born alive	10.19
Average number pigs weaned	8.84
Average weaning weight, pounds, 56 days	44.26
Average 154-day weight, pounds	198.10
Average feed per 100 pounds of gain, weaning to 198 pounds	316.00

needs to run for ten or twenty generations, but the data accumulated are very encouraging.

AN OVER-ALL PROGRAM

The most important recent contributions to animal improvement indicate clearly that the most productive commercial animals will be produced by some system of crossing; that improved lines for crossing will come from a program which combines crossing, careful performance testing, and inbreeding; and that genetic diversity is a big factor in promoting hybrid vigor.

These indications provide material for very serious thought and planning by those designing long-time programs for improvement. Aftersight is always better than foresight; otherwise there would be no need for research; a fair criticism may be made, however, of all programs for the development of inbred lines and their ultimate uses in crossing with which the author is familiar: that they are organized on too narrow a genetic base and they have grown too much as "Topsy" grew. That was excusable in the past, because the researchers were working for leads and openings and were forced to work with materials on hand.

In the light of experience with this type of work and in the light of research in corn breeding new programs should be organized about as follows:

1. Draw on rather widely divergent sources for genetic material.
2. Obtain as much information as possible regarding the characteristics of each of the genetic materials to be used.
3. Obtain as much information as possible regarding the results of crossing the different foundation stocks.
4. Arrange the foundation stocks so that those combined for the development of inbred lines will not be crossed later on with themselves. Such a plan is illustrated in Fig. 112. The illustration simplifies the problem, because actually not all the lines started will be developed into useful lines nor will all the new lines cross to advantage. If, therefore, the plan can be multiplied by 2, 3, 4, or 5, the likelihood of its success will increase proportionately.

It is not to be expected that the completely perfect crossing combination of lines will ever be developed. For that reason, effort will always be needed to further improve lines for crossing. Once, however, three good crossing lines become identified, it appears that the breeder will probably make more progress by

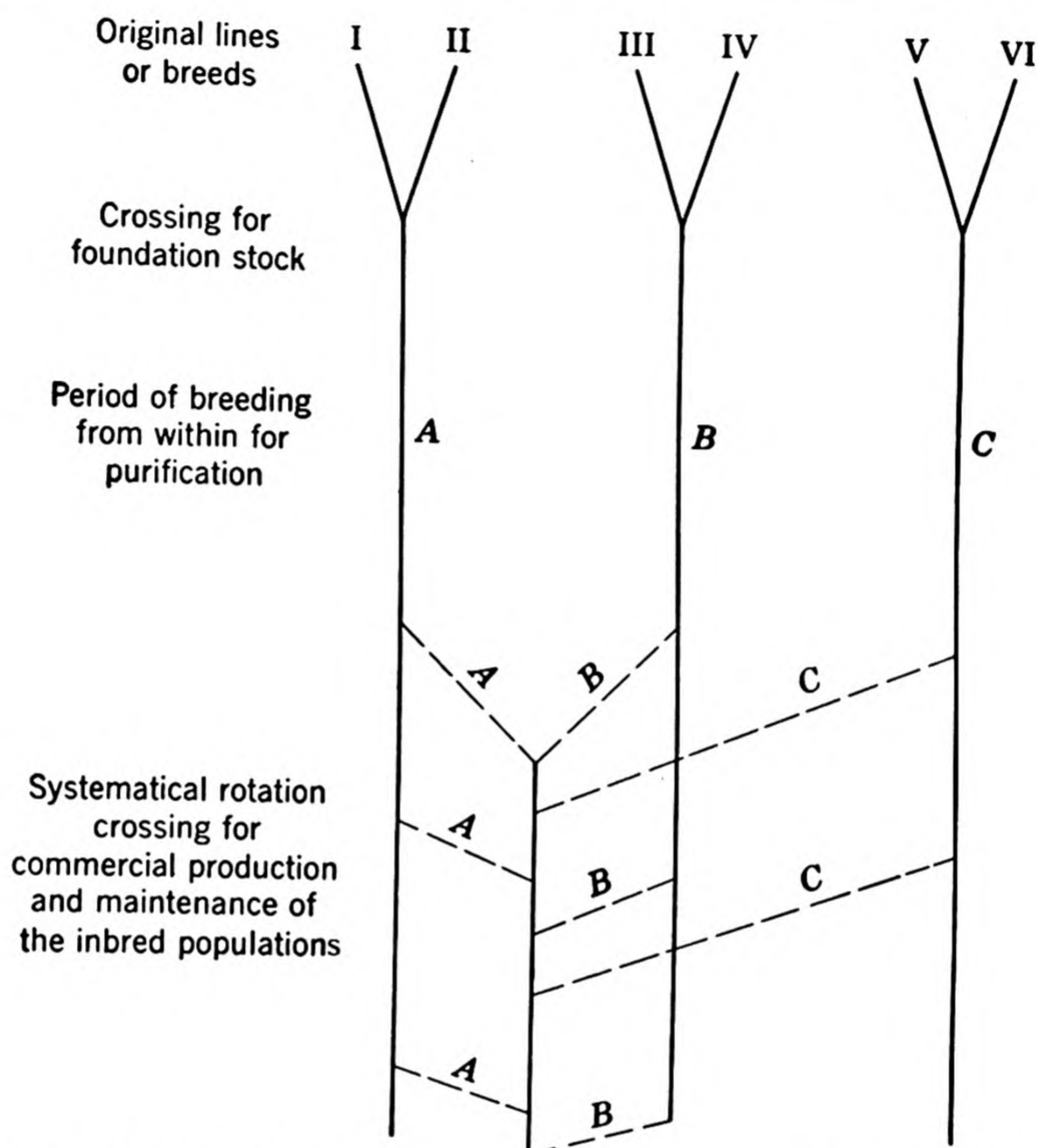


FIG. 112. A plan for the development of inbred lines from crossbred foundations, yet having lines that differ in their genetic backgrounds.

improving his existing lines that are already crossing well than by searching for entirely new lines. For the improvement of the lines being used, any one of the methods suggested and discussed in this chapter offers possibilities.

Incross Males. Incross animals are produced by crossing two recognized inbred lines. Incross males are finding considerable favor with commercial producers. They are more vigorous than inbred males. Being more vigorous, they will take somewhat rougher treatment and appear to be doing a somewhat better job of getting females settled.

If incross males prove to be the most satisfactory method of utilizing inbred lines, the program outlined above will require some expansion; six inbred lines or breeds will then be required to carry out the complete program. Since, as outlined above, each inbred line was to arise from the crossing of two breeds, this program would necessitate the use of twelve breeds at the outset. It does not appear that it would be practicable to carry the program to that extreme. If, however, twelve promising breeds, each of which differed from the others, were available as foundation material, it should offer maximum opportunities. It does not appear, however, that this is likely to be the case. For this reason, some slight overlapping of breeds may become necessary and, in some cases, the incross males may best be produced by crossing two inbred lines within a single breed. This then allows the wider cross to be made by the commercial producer.

Final Summation of Both New and Old Methods. In the final analysis breeding is an attempt by man to gain control over the gene combinations used. Man does not know how to make or even to modify genes at will; therefore, the breeder's job is to gain a mastery over those already in existence. All old and new methods are designed to that end; in some manner or other, all of them use one or more of the breeder's three tools—cross-breeding, inbreeding, and selection. It is not likely that there is, or ever will be, any one *best* method.

The breeder and critic alike should always keep in mind, however, that the final appraisal of the value of a method or line of breeding must come from what it will do on the job for which it was designed.

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Glossary

- Aberration.** An irregularity in chromosome distribution during heterotypic or homotypic cell division.
- Abortion.** A miscarriage during prenatal development.
- Acquired character.** A change of the structure or function of an organism which has been brought about during the life of the individual.
- Allelomorph.** One of a pair of contrasted factors occupying the same locus in homologous chromosomes and determining the development of contrasted characters.
- Anastomosis (vascular).** The union of two normally distinct vascular systems.
- Atavism.** The appearance of ancestral characters in an individual; characters possessed by ancestors less distinctly removed than in reversion.
- Autosome.** Any chromosome other than the sex chromosomes.
- Back cross.** A cross between a hybrid and either of its parental types.
- Balanced lethals.** Lethal factors located in chromosomes of opposite gametes and each lethal closely linked with the normal allelomorph of the other lethal. Thus crossing-over is infrequent, and generally no obvious harm results from the lethals.
- Biometry.** The branch of science dealing with the statistical investigation of organic differences.
- Bivalent (chromosomes).** A pair of homologous chromosomes.
- Breed.** A group of individuals having a common origin and possessing certain distinguishing characteristics not common to other members of the same species.
- Breeding.** The art of improving animals and plants.
- Cell.** Any one of the minute protoplasmic bodies of which an organic tissue is built.
- Cervix (uteri).** The neck or lower end of the uterus leading into the vagina.
- Character.** One of the many details of form, structure, substance or function which, taken collectively, constitute the individual.
- Chromatin.** The principal substance from which chromosomes are formed, so called because of the readiness with which it becomes stained by certain dyes.
- Chromosome.** A minute structure composed largely of chromatin, having a rather definite and characteristic size and shape at certain stages of cell development, the cell of each species containing a definite number of chromosomes. (In certain species it may be that one sex has one more chromosome than the other.)

Colostrum. The milk, produced for a few days after parturition, carrying a higher percentage of protein and minerals than later drawn milk.

Cytology. The study of the cells, with especial regard to their internal structure.

Cytoplasm. The cell protoplasm outside the nucleus.

Dam. The female parent.

Development. The complete growth, physical, mental, and functional, of the individual from fertilization to maturity.

Diluting factor. A minor factor which by itself has no noticeable effect but which lessens the effect of another factor.

Diploid. The condition in which both members of each chromosome pair are present; the chromosome number which usually and normally occurs in the somatic cell of a species, twice the gametic or haploid number.

Dominant. A term applied to the member of an allelomorphic pair which manifests an effect wholly or partly to the exclusion of the effect of the other allelomorph.

Dominance. Dominance may be complete, partial, absent, or greater than complete. In the latter case it is known as overdominance and is due to the *Aa* condition yielding more than *AA*.

Drosophila. The pomace or fruit fly.

Egg. The ovum or female germ cell.

Environment. The sum total of the external influences.

Epistatic. That condition in which one factor prevents a factor other than its allelomorph from exhibiting its normal effect on the development of the individual.

Factor. A unit of inheritance occupying a definite locus on one or both members of a definite chromosome pair, the presence of which is responsible for the development of a certain character or modification of a character of the individual which possesses that genotype; a determiner, or gene.

Family. A group of individuals within a breed, all of which have pedigrees which trace directly in the female line to a common ancestress called the foundress of the family. At times used in reference to the male line of descent, in which case it is used interchangeably with line of breeding.

Fertility. The ability to produce normal young.

Fertilization. The union of male and female gametes.

Foetus. The unborn young during about the last two-thirds of its development within the uterus.

Gamete. A mature male or female productive cell.

Gametogenesis. The process by which mature sex cells are developed from the primordial germ tract.

Gene. See Factor.

- Gene complex.** The balanced state of several (perhaps many) genes which collectively affect a given character or group of characters.
- Gene interaction.** The action of different genes upon each other.
- Genotype.** An individual's constitution as regards the factors composing its germ plasm; the hereditary factors which it may transmit to its offspring.
- Germ cells.** *See* Gamete.
- Germ plasm.** The cell protoplasm which is the material basis of heredity and is transmitted from one generation to another.
- Gonads.** The glands which produce the reproductive cells.
- Grade.** An individual, one of whose parents is a purebred, usually the sire, and the other a scrub or grade.
- Haploid.** The usual chromosome number occurring in the gametes in which only one member of each chromosome pair is present; one-half the diploid number.
- Hermaphrodite.** An individual possessing both male and female sex organs which are capable of functioning.
- Heterotypic division.** The true division of reduction by which the homologous chromosomes are separated into different gametes.
- Heterosis.** The increased stimulus for growth and vigor often exhibited by the crossbred individual; hybrid vigor.
- Heterozygote.** An individual which has resulted from the fusion of gametes carrying allelomorphic genes.
- Heterozygous.** A condition in which the homologous chromosomes carry dissimilar genes.
- Homologous chromosomes.** The members of a chromosome pair.
- Homozygote.** An individual which has resulted from the fusion of gametes carrying identical genes.
- Homozygous.** A condition in which the homologous chromosomes carry similar genes.
- Hormone.** A substance produced by one organ, supposedly carried by the blood stream to another organ or tissue on which it has a specific effect; it may stimulate or inhibit functional activity, depending upon its nature.
- Hybrid.** An individual resulting from the mating of individuals belonging to different genotypes.
- Hypostatic.** That condition in which a factor is prevented from exhibiting its normal effect in the development of the individual due to the presence of some factor other than its allelomorph. Contrast with epistatic.
- Inbreeding.** The mating of related individuals.
- Indigenous.** Native, not introduced from foreign territory.
- Inheritance (genetic).** The transmission of genetic factors from parent to offspring.
- Inter se.** Among themselves.
- In utero.** In the uterus.

Lethal. Destructive of life.

Line of breeding. A rather indefinite term used somewhat loosely, applied to a group of individuals which have descended from one individual; used more frequently and correctly with reference to male lines of descent. More recently it is used to designate an inbred and closely related family.

Linkage. A form of inheritance in which certain genes tend to remain together in the process of segregation and transmission from one generation to the next, owing to their being located on the same chromosome.

Locus (*pl.* loci). A definite point or region in a chromosome at which a genetic factor is located.

Metabolism. The absorption and utilization of the digested nutrients for the building of body tissue or for bodily functions and also the breaking down of bodily tissue into non-living matter.

Multiple factors. Two or more factors all of which are needed to produce a maximum effect.

Mutant. An individual the genotypic constitution of which differs from that of its parents and ancestors because of a definite change in the germ plasm, not brought about by segregation or crossing-over.

Mutation. The process by which a mutant is produced.

Neolithic. An early stage of human culture or development following the Paleolithic period; the later Stone Age.

Nucleus. That part of the cell which is located more or less centrally and contains the chromatin.

Oögenesis. The process by which ripe germ cells are produced by the female.

Ovotestis. A gonad, part of which is composed of ovarian tissue and the rest of testicular.

Ovum (*pl.* ova). The female germ cell.

Paleolithic. The stage of human culture or development preceding the Neolithic period; the early Stone Age; the earliest known stage of human culture.

Pedigree. A list of the individual's ancestors, usually only those of the five closest generations.

Phenotype. An individual's constitution in regard to the visible characters; contrast with genotype.

Prepotency. The ability possessed by certain individuals to impress their characteristics upon their offspring to a marked degree.

Produce. A female's offspring.

Purebred. An animal which is registered or eligible to registration in the record books of its breed; it is the descendant, in all lines of its ancestry, of individuals of the same type as itself.

- Pure line.** A strain that has resulted from continued inbreeding, the individual members of which are closely related and highly purified.
- Recessive.** The opposite of dominant.
- Reversion.** The appearance in an individual of a character possessed by some distant ancestor.
- Scrub.** An animal of nondescript breeding and having no definite type; a decidedly inferior individual.
- Segregation.** The process by which genetic factors become separated and included in different gametes by the process of gametogenesis.
- Sex chromosome.** A chromosome other than the autosomes and one which has been identified with one or the other of the sexes; one member of a pair of chromosomes which differ morphologically or physiologically from the autosomes and carry a factor or factors for sex.
- Sex-limited.** Applied to characters which are exhibited by one sex only.
- Sex-linked.** Applied to factors located on the sex chromosome or to the characters conditioned by them; the linkage of a factor with the factor or factors concerned with sex determination.
- Sex ratio.** The proportion of males to females of a population.
- Sire.** The male parent.
- Soma.** The body; in contrast with the germ or germ plasm.
- Somatoplasm.** The body tissues.
- Species.** A group of animals or plants which have in common one or more distinctive characters by which they may be differentiated from other species; a subgroup of a genus but usually including several breeds or varieties.
- Spermatogenesis.** The process by which ripe germ cells are produced by the male.
- Spermatozoon** (*pl.* spermatozoa). The male germ cell; the sperm cell.
- Sterility.** Inability to produce normal living young.
- Strain.** A rather loose term applied to a group of individuals within a breed and differing in one or more characters from the other members of the breed, for example, the Milking Shorthorns or Polled Herefords.
- Tetraploid.** Double the diploid number of chromosomes characteristic of the species.
- Tribe.** A combination of one or more families, the foundresses of which trace in the female line to a common ancestress which is the foundress of the tribe.
- Type.** An ideal presumably embodying all the characters contributory to the animal's value for some certain purpose or purposes.
- Univalent.** An unpaired chromosome. Contrast with bivalent.

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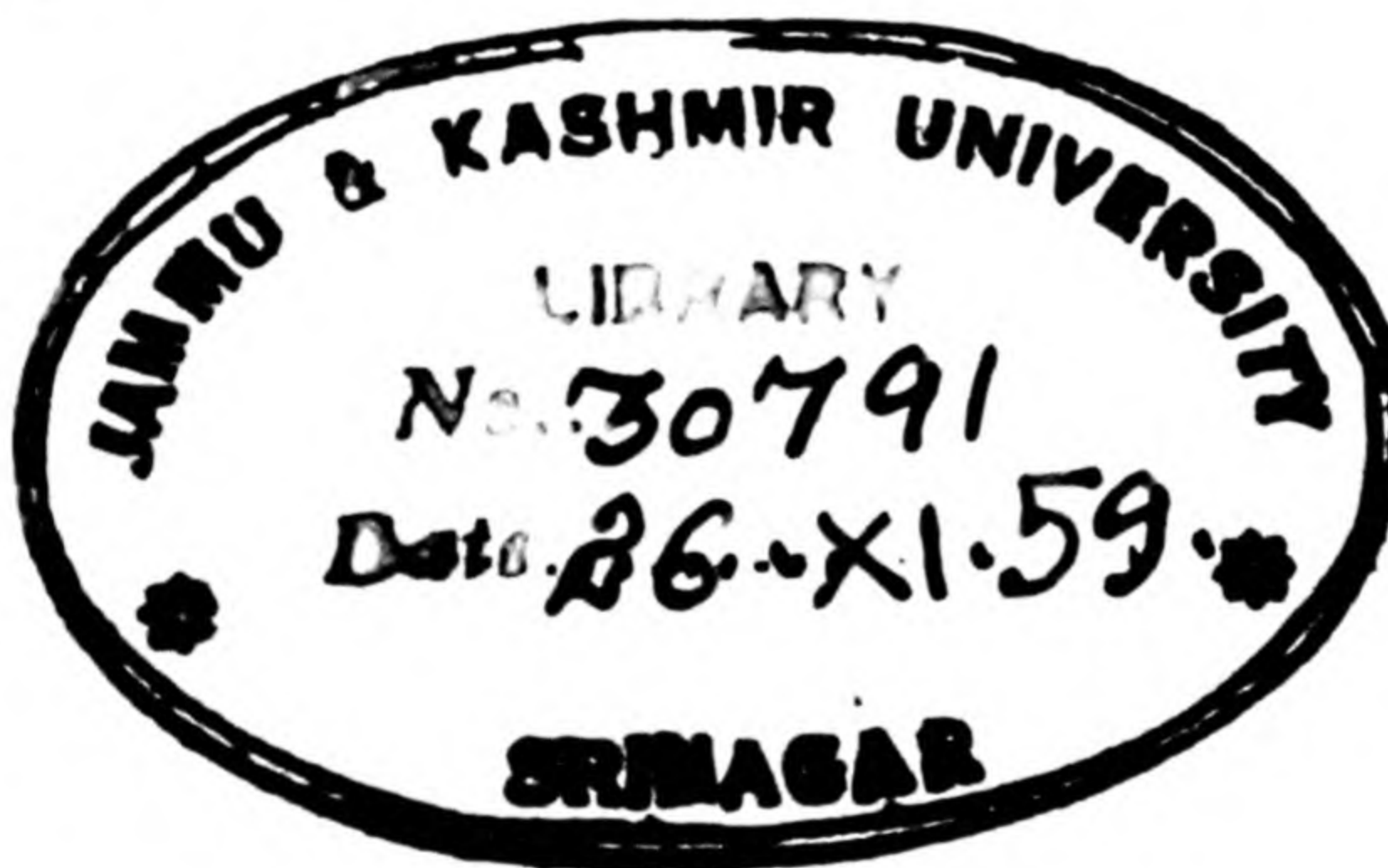
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